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A link between plant scientists in all branches and in all countries

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FIGURE 1.— NIKOLAI IVANOVICH VAVILOV was born in Russia in 1887. Studied with WILLIAM BATESON at the John Innes Horticultural Institution and with Sir ROWLAND BIFFEN at the School of Agriculture, Cambridge, England, 1913-1914. Professor, Moscow University, 1914. Expedition to Persia and surrounding countries to collect cereals, 1916. Professor of Agriculture, Botany, and Genetics, Saratov, 1917. President of the Lenin Academy of Agricultural Sciences and Director of the Institute of Applied Botany (Institute of Plant Industry), 1921. Establishment and direction of more than four hundred research institutes and experiment stations with staff of 20,000, 1921-1934. Expeditions to Afghanistan, Abyssinia, China, Central America, and South America to collect economic plants, including 26,000 strains of wheat, 1923-1931. Direction of comprehensive study of the world collection of plants, and use of these in breeding; similar works with livestock, including horses, cattle, and reindeer, 1931-1939. Elected Academician of the USSR, 1929. Soviet delegate to International Congress on the History of Science, London, 1931. Invited to be President of International Congress of Genetics, 1939. Elected Foreign member of the Royal Society of Great Britain, 1942. Died probably in the early months of 1942.

Рис. 1. Гомологические ряды изменчивости у видов пшеницы и ячменя по признаку остистости. 1—4—Формы ряда мягких пшениц (42 хромосомы): остистая, короткоостая, инфлятная (Иран) и безостая; 5—8 формы ряда твердых пшениц (23 хромосом): остистая, короткоостая (Абиссиния), инфлятная (Абиссиния) и безостая (Абиссиния) и 9—10 формы шестирядного ячменя: остистая, короткоостая (Япония), инфлятная (*trifurcatum*) из северной Индии и безостая (Япония).

Рис. М. П. Лобановой.

FIGURE 2.—Homologous series of variations in species of wheat and barley, with respect to awnedness. 1-4, forms of soft wheat (42 chromosomes): awned, short-awned, inflated (Iran), and awnless; 5-8, forms of hard wheat (28 chromosomes): awned, short-awned (Abyssinia), inflated (Abyssinia), and awnless (Abyssinia); 9-12, forms of six-rowed barley: awned, short-awned (Japan), inflated (*trifurcatum*) from northern India, and awnless (Japan). Drawn by M. P. LOBANOVA.

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(Issued Spring 1951)

The ORIGIN, VARIATION, IMMUNITY and BREEDING of CULTIVATED PLANTS

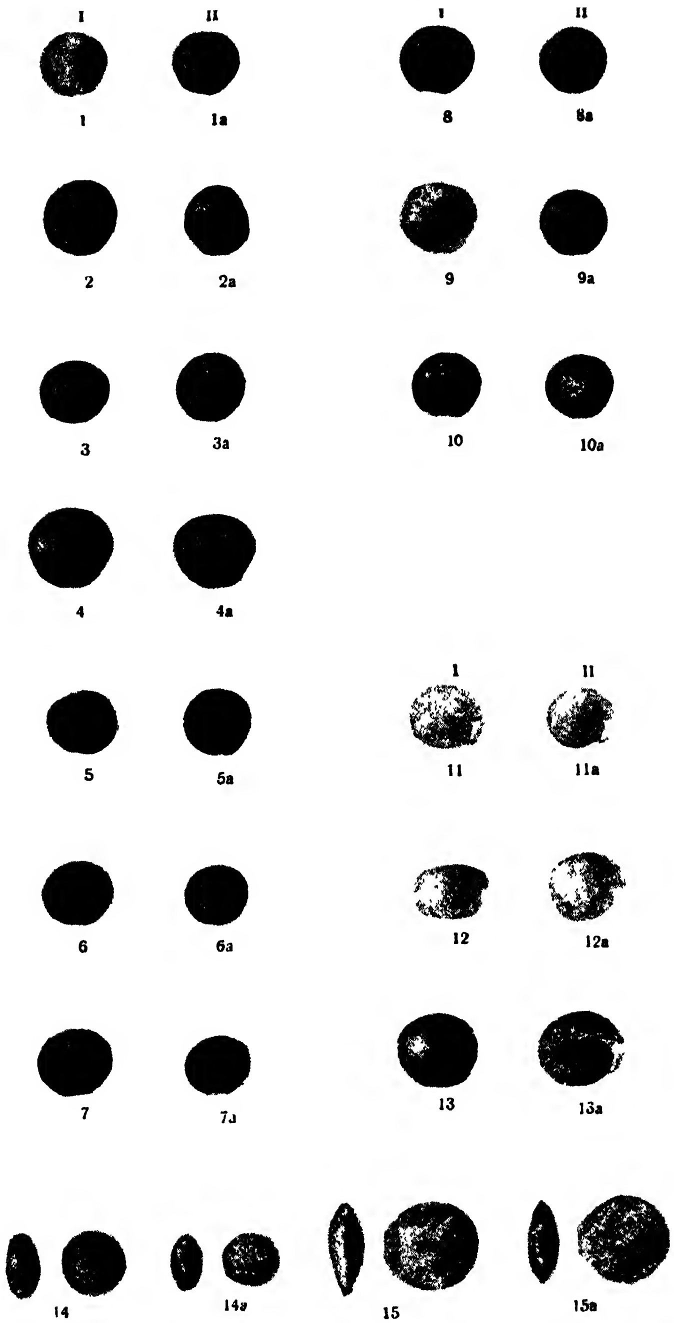

FIGURE 3.—Homologous series of heritable variations in seed and cotyledon in forms of vetch (*Vicia sativa* L.) and lentil (*Lens esculenta* Moench.). Enlarged two diameters. Drawn by M. P. LOBANOVA *From left to right:* Seed form in I. Vetch, II. Lentils; Cotyledons in I. Vetch, II. Lentils.

I. Vetch: 1. Kharkov; 2. Kharkov; 3. Kharkov; 4. *Vicia platysperma* Bar., Saratov (Flat-seeded, disk-like type); 5 Kharkov; 6. Kharkov; 7. Kharkov; 8. Saratov; 9. Kharkov; 10. Saratov (Wildling), 11. Kharkov; 12. Central Asia; 13. Kharkov; 14 Small-seeded type of Russian fodder vetch; 15. *Vicia platysperma* Bar., Saratov (Flat-seeded, disk-like type).

II. Lentils: 1a. *Vicia persica* Bar., Persia; 2a. Palestine; 3a. *Vicia grisea* Bar., Asia Minor; 4a. *Vicia nummularia* Al., Saratov (Flat type); 5a. *Vicia violascens* Bar., Armenia, 6a. *Vicia brunnea* Bar., Georgia (SSSR); 7a. *Vicia melanosperma* Bar., Afghanistan (Black-seeded); 8a. *Vicia syriaca* Bar., Syria; 9a. *Vicia indica* Bar., India; 10a. *Vicia marmorata* Bar., Asia Minor; 11a. *Vicia dupuyensis* Bar., France ("DuPuy"); 12a. *Vicia abyssinica* Al, Abyssinia; 13a. *Vicia leucosperma* Tschern., Kiev (Green-seeded); 14a. *Vicia vulgaris* (Al.) Bar., Ryazan (SSSR); 15a. *Vicia nummularia* Al., Saratov (Disk-like).

The ORIGIN, VARIATION, IMMUNITY and BREEDING *of* CULTIVATED PLANTS

Selected Writings

of

N. I. VAVILOV

translated from the Russian

by K. STARR CHESTER, PH.D.

Supervisor of Agricultural Research,
Battelle Memorial Institute, Columbus, Ohio.

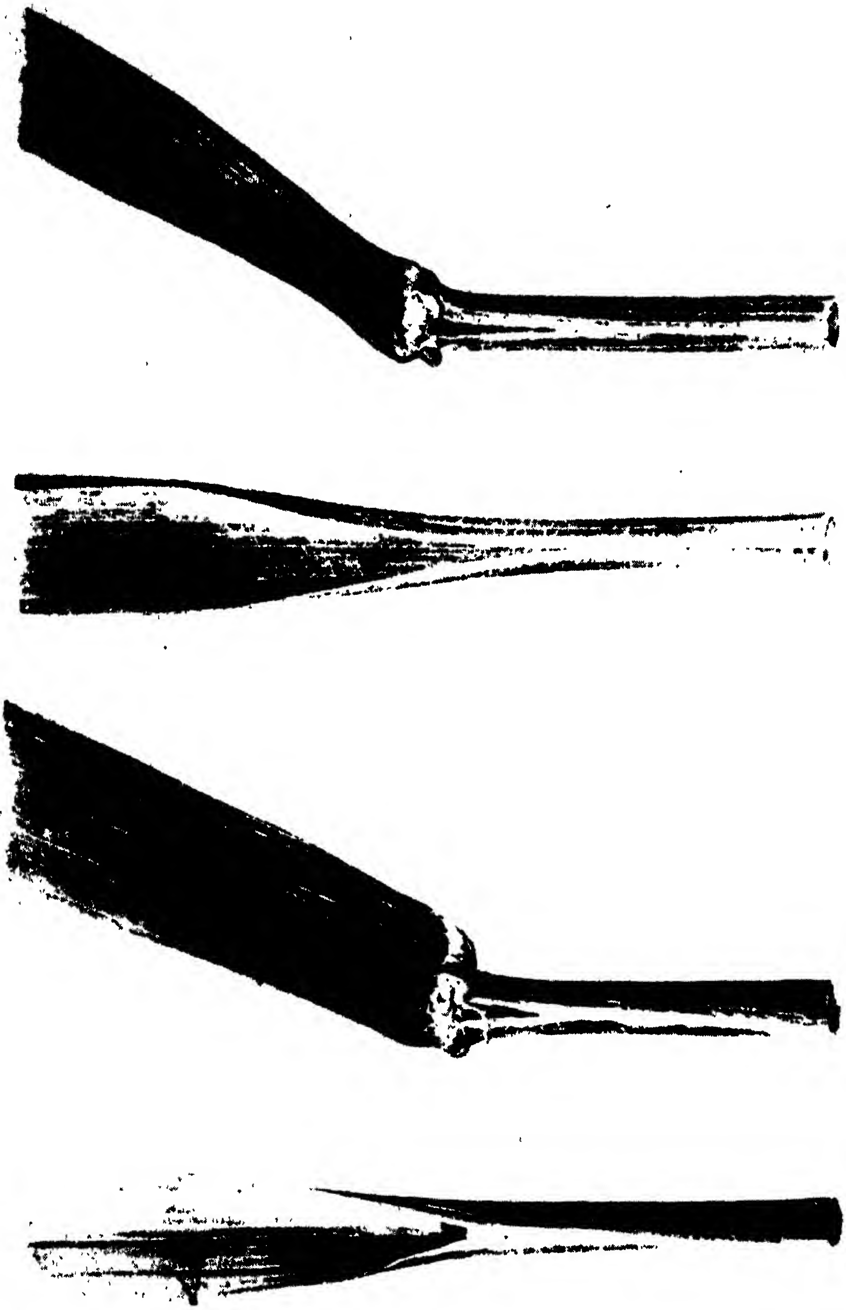

FIGURE 4.— Eligulate wheat, *Triticum vulgare eligulatum* Vav., found in North Afghanistan and in Palmyra; b) wheat with ordinary ligula, *Triticum vulgare ligulatum;* c) eligulate rye, *Secale cereale eligulatum* Vav. found in North Afghanistan and in Palmyra; d) ordinary rye, *Secale cereale ligulatum.*

PREFACE

Acad. NIKOLAI IVANOVICH VAVILOV *will long be remembered as one of the world's outstanding contributors to scientific thought and accomplishment in genetics, plant breeding, and the study of plant variation, systematics, and evolution.*

In 1935 the climax of his career was marked by publication of the 2500-page symposium, The Scientific Bases of Plant Breeding *of which* VAVILOV *was editor and a principal author. Here, in their last and most complete form, are given* VAVILOV'S *contributions on the origin of cultivated plants, the law of homologous series in variation, the immunity of plants from diseases, and the scientific bases of wheat breeding.*

VAVILOV *had hoped to translate at least a part of these contributions into English for the benefit of his many English-speaking fellow scientists and friends, but this was prevented by his untimely death, and, until the present, these classics of botanical-agricultural literature, in their mature form, have been printed only in the Russian tongue. They are translated here in full.*

VAVILOV'S *life and achievements are an inspiration and a challenge to the generations of scientists who follow the trails which he has blazed. These translations are offered in the hope and belief that those who were not privileged to have known* VAVILOV *may find their scientific experiences enriched, their minds stimulated, and their research energized by better acquaintance with the work and the philosophy of one of the most memorable figures in the history of plant science.*

A number of colleagues have contributed to the preparation of this volume. With kind permission of Dr. E. W. BRANDES *of the U. S. Department of Agriculture and Mrs.* EUGENIA ARTSCHWAGER, *the latter's mimeographed translation of most of the chapter on the phytogeographic bases of plant breeding was made available for consultation, as was a typed partial translation of the same chapter and of the introductory chapter, kindly furnished by Dr.* R. H. RICHENS *of the Commonwealth Bureau of Plant Breeding and Genetics, Cambridge. The text of the introductory pages is essentially as received from Dr.* RICHENS. *The assistance of each of these is gratefully acknowledged. Thanks is also expressed to the Editor of* CHRONICA BOTANICA *for his encouragement of the project and his valuable assistance.*

K. STARR CHESTER.

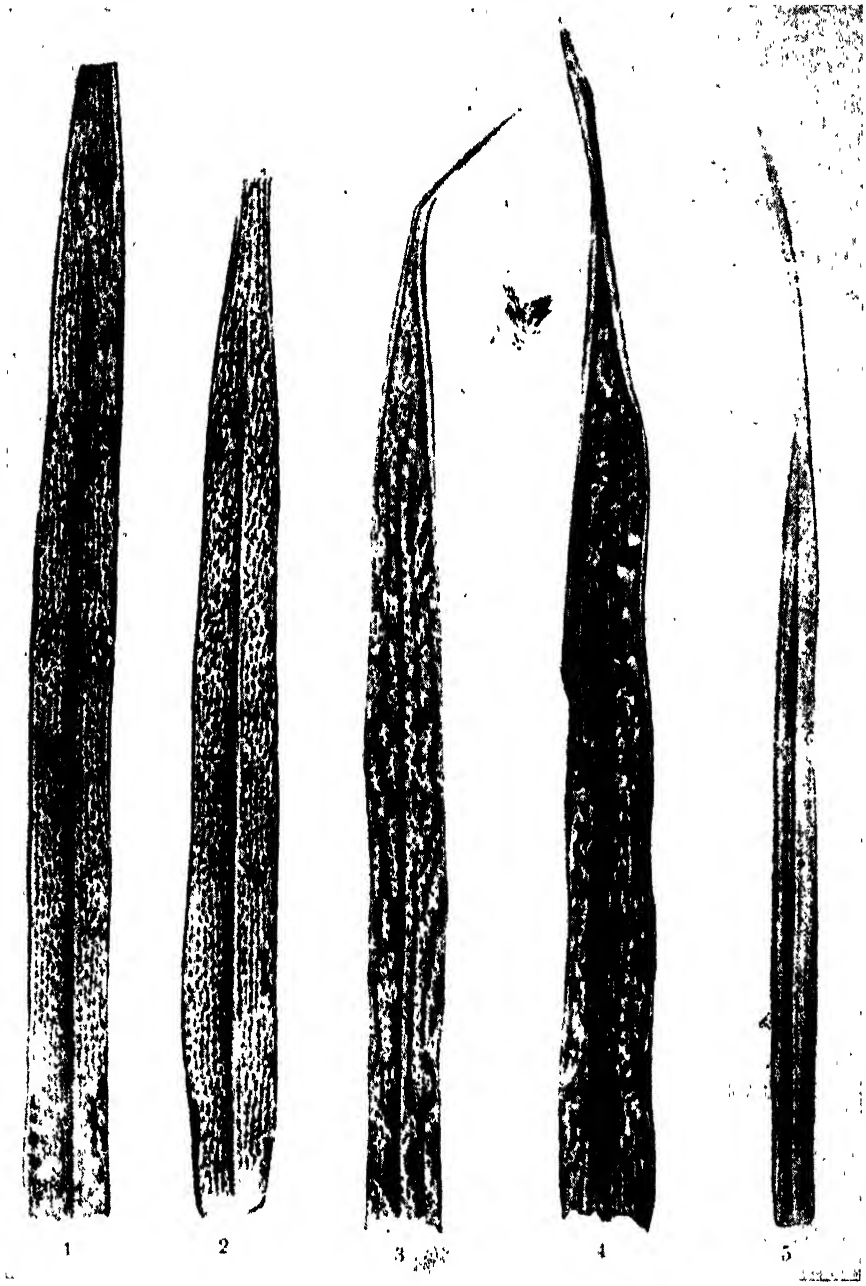

FIGURE 5.— Scale of resistance of wheat varieties (the comparative resistance of wheat varieties to leaf rust, *Puccinia triticina* Eriks., showing the upper sides of leaves of the second rank from the top).— (1) Strongly attacked variety No. A-127, *T. vulgare* Vill. var. ***ferrugineum*** Al. (Rust value — 4). The figure shows the maximal degree of susceptibility to leaf rust in a leaf of a highly susceptible variety — (2) Strong attack of the variety A-2761, *T. vulgare* var. ***erythrospermum*** Kcke. (Rust value — 4). The figure shows the ordinary degree of attack of leaf rust on a strongly susceptible variety.— (3) Moderately affected variety A-191, *T. vulgare* var. ***ferrugineum*** Al. (Rust value — 3). The small size of the fungus pustules and the yellow spots bordering them are very characteristic.— (4) Weakly attacked variety A-2751, *T. durum* Desf. var. ***hordeiforme*** Host. (Rust value — 2). A very typical picture of attack of leaf rust on durum wheats.— (5) The most resistant variety No. A-81, *T. monococcum* L. var. ***flavescens*** Kcke. Rust value — 0).

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FIGURE 6.— Scale of resistance of wheat varieties (the comparative resistance of varieties of spring wheat to stripe rust, *Puccinia glumarum* Eriks., showing the upper sides of leaves of the second rank from the top).— *Rust value 4* — strongly attacked variety No. 441, *T. vulgare* var. *erythrospermum* Kcke., showing the maximal degree of attack of stripe rust on leaves of a susceptible variety under field conditions. *Rust value 3* — moderately attacked variety No. 78, *T. vulgare* var. *ferrugineum* Al., characterized by the smaller size of the fungus pustules and the presence around them of yellow spots of injured leaf tissues. *Rust value 2* — weakly attacked variety No. A-2751, *T. durum* Desf. var. *hordeiforme* Host. Typical picture of attack of stripe rust on durum wheat. *Rust value 1* — very weakly attacked variety No. 2759, *T. vulgare* var. *milturum* Al. *Rust value 0* — most resistant variety No. 59, *T. monococcum* L. var. *hornemanni* Glem., einkorn.

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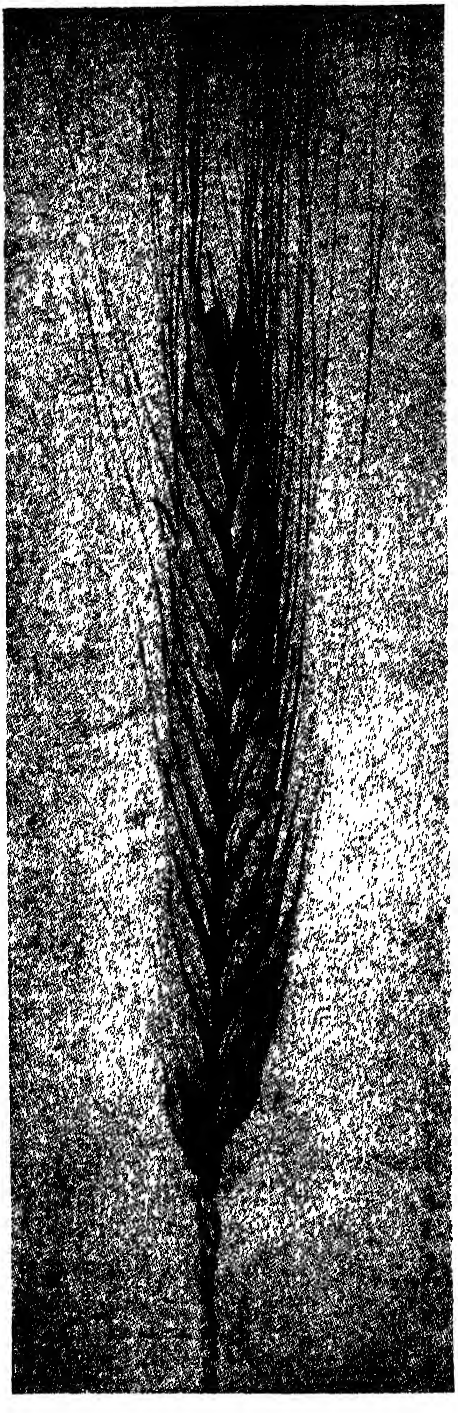

FIGURE 7.—*Triticum polonicum abyssinicum* var. *sporadicum* Vav. et Fortun. Abyssinia, Chechersk region. Original photograph.

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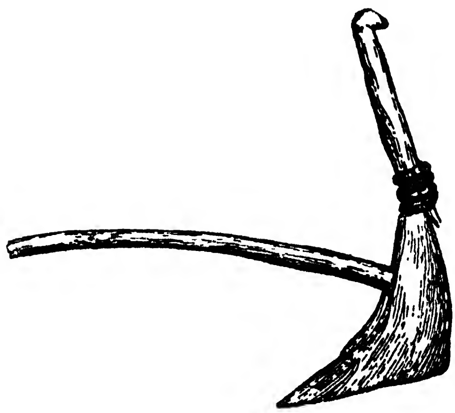
— *Vignettes from Vavilov and Bukinich's 'Agricultural Afghanistan' (1929)* —

"WE ARE NOW ENTERING AN EPOCH OF DIFFERENTIAL ECOLOGICAL, PHYSIOLOGICAL, AND GENETIC CLASSIFICATION. IT IS AN IMMENSE WORK. THE OCEAN OF KNOWLEDGE IS PRACTICALLY UNTOUCHED BY BIOLOGISTS. IT REQUIRES THE JOINT LABOURS OF MANY DIFFERENT SPECIALISTS — PHYSIOLOGISTS, CYTOLOGISTS, GENETICISTS, SYSTEMATISTS, AND BIOCHEMISTS. IT REQUIRES THE INTERNATIONAL SPIRIT, THE CO-OPERATIVE WORK OF INVESTIGATORS THROUGHOUT THE WHOLE WORLD . . . . . . WE DO NOT DOUBT THAT THE NEW SYSTEMATICS WILL BRING US TO A NEW AND BETTER UNDERSTANDING OF EVOLUTION, TO A GREAT INCREASE IN THE POSSIBILITIES OF GOVERNING THE PROCESSES OF EVOLUTION, AND TO GREAT IMPROVEMENT IN OUR CULTIVATED PLANTS AND DOMESTIC BREEDS OF ANIMALS. IT WILL BRING US LOGICALLY TO THE NEXT STEP; INTEGRATION AND SYNTHESIS." (*From the last publication of Vavilov in "The New Systematics," Oxford, 1940*).

PLANT BREEDING

as

A SCIENCE



Plant breeding is a science, an art, and a branch of agricultural practice.

As an art its origins go back to the beginning of agriculture when plants were first cultivated and animals domesticated. The history of animal and crop husbandry reveals the supreme importance of plant breeding as an art, which by means of the guidance of the living organism strives to gain such control over animals and plants as contributes increasingly to the satisfaction of human needs.

Comparison of modern cultivated breeds and varieties with their original wild forms, still to be found in nature, shows how great is the progress which has resulted from man's interference. For hundreds and thousands of years many species and varieties of wheat have existed which are the product of selection by unknown breeders in ancient times. To this day in Peru, varieties of corn, included in the Cuzco group, are grown which have grain three or four times as large as those of the usual varieties of the cultivated crop. Excavations have shown that a corn variety with large grain existed at least a thousand years ago, and was known to the Incas. Its size has not been exceeded by any produced by the plant breeder of today.

Some of the best modern varieties of cotton as, for example, the upland varieties widely grown in the U. S. A. and in the Soviet Union, resulted from minute selection and propagation of varieties acquired by Americans from peasants living in old Mexican villages. Such varieties are Acala, Big Boll, and Durango which doubtless were bred by unknown breeders, and date back to the Maya civilization which survived until the coming of the Europeans.

Old districts of Turkey and of our Khiva oasis are world-famous for their melons which, bred by unknown breeders hundreds and perhaps even thousands of years ago, are unsurpassed to this day. A large number of the most valuable varieties of fruit trees of the present time are the creation of the art of the plant breeder. Many of the best varieties of pears, apples, and grapes originated in remote ages.

The world's *chef d'oeuvre* of plant breeding is to be found on the island of Sakurajima in southern Japan: a radish one *pud* in weight (15 to 17 kgs.). On the same island under conditions similar to those in which it thrives, are a wild radish and a cultivated radish, each related to the same botanical species, which form only small roots. It would be vain then to ask how the wonderful giant has been produced; no one knows, not even the professor of plant breeding who lives on the neighboring island of Kagoshima. But one thing is certain, the giant forms were the consequence of skillful selection of extreme variants by unknown breeders many ages ago. An interesting principle is deducible from a comparison of ancient farming civilizations; the higher the technical level of a civilization the more highly bred are its crop plants. Thus, Chinese vegetables including different varieties of cabbage, soybeans, rice, and many crops of Mediterranean countries, where the powerful civilizations of the Old World once thrived, are noteworthy for quality and size of fruit and seed, and altogether bear witness of careful selection during many centuries. In Algiers in the gardens of natives we collected onion bulbs which weighed up to two kilograms and flax seeds twice as large as those of normal size. Similar phenomena were evident to a still more striking extent in wheat, beans, lentils, and grain. On the other hand, in many regions, in northwest India, Afghanistan, and Abyssinia, and in Peru and Bolivia, among the pre-Inca civili-

zations preserved in the mountainous regions of the Andes, the plant varieties are small, unfruitful, poor in quality, and but little different from the wild forms which often grow in fields nearby, in uncultivated land and field borders.

Breeds of livestock and varieties of crop plants, which have survived to our time, bear traces of the skill of unknown breeders. Instructions on breeding given two thousand years before our epoch are to be found in the works of COLUMELLA, VARRO, VIRGIL, and THEOPHRASTUS.

In a still larger measure, the more fully recorded history of recent times reveals the part played by breeding as an art: the great variety of new ornamental plants which have come into existence, the striking results obtained from flower breeding generally during the last century as exemplified in new varieties of roses, dahlias, chrysanthemums, tulips, cannas, and gladioli, all of which bear eloquent testimony to breeding as an art. In *The Variation of Animals and Plants under Domestication,* DARWIN gives an excellent summary of such results.

The advancement of capitalism at the end of the XVIIIth century and the beginning of the XIXth century in Western Europe, particularly in England, and the opening up of markets necessary for a new world economy, gave a fresh stimulus to pedigree livestock and seed production, thus affording profitable outlets for its development. The progress of pedigree livestock breeding was assisted by land enclosure in England at the end of the XVIIIth century, intensification of farming, and introduction of crop rotations which provided a large proportion of forage grasses and root crops. England at this time established a monopoly of new breeds. BAKEWELL originated new breeds of sheep and the brothers CHARLES and ROBERT COLLING obtained the celebrated breed of Shorthorns. England was then, in fact, the source of improved breeds for the whole world. Numerous societies sprang into being for the promotion of pedigree livestock breeding; hundreds of clubs were founded for the study and judging of new breeds of horses, cattle, dogs, and poultry. Increased interest also was taken in the investigation of new crop varieties. Large seed and industrial plant breeding firms were established. In 1727, near Paris was founded the famous seed firm of Vilmorin which exists to this day and is the chief supplier of seeds in France and her Colonies. During the XIXth century thousands of seed firms, both large and small, appeared in Germany, England, and the United States.

As farming became more intensified, as fertilizers entered more widely into use, and as new machines and implements were employed, the demand for new varieties considerably increased. Breeding was eagerly taken up by those engaged in crop and animal husbandry and farming on a large scale, and was developed on capitalist lines to the fullest possible extent. It then became commercially profitable and in the course of time was mechanized. In these circumstances skilled workers were called for. Breeding had now to be associated with the mass production of pedigree seed and livestock. Factories were set up with the labor and equipment requisite for extensive serial output. In Germany, for example at Kleinwanzleben, the breeding of sugar beet, which involves the analysis of millions of roots yearly, is mechanized to a remarkable extent. Analytical laboratories, in no way differing from factories, have been erected; to these are laid rails along which trucks loaded with roots are carried. Such buildings are designed to facilitate the speedy washing and analysis of roots. From an art, breeding has thus to a large extent become an industry or a trade.

With the advance of technique, processes of selection became increasingly mechanized. NEERGAARD, the engineer, who is director of the famous Svalöv

agricultural experimental station in Sweden, invented a special apparatus for speeding up the measuring processes involved in the determination of weight, number and volume. A period of invention set in. Numerous mechanical devices for plant breeding were designed: special drills, threshers, cleaners, and graders. A technique of breeding is in process of being worked out; in other words, mechanization in a semi-industrial form is being applied. Such development is especially noticeable in regard to sugar and forage beets.

The idea of breeding with which large firms in western Europe, and particularly England, were preoccupied in the early XIXth century, was transformed by the genius of DARWIN in his theory of natural selection and its part in evolution. The social genesis of his work is revealed in every detail of it. As we know, he utilized the practical experience of animal and crop husbandmen in improving varieties and breeds, and thus for building up his conception of evolution acquired a large amount of information which he supplemented with the conclusions arrived at from a study of plants and animals in nature. His theory provided the first scientific basis for the breeding of plants and animals. From our point of view, his greatest service consisted in that he opened the way to the limitless influence of human reason and will on the variability of plants and animals. His study of evolution became the primary basis of scientific breeding.

Experimental research in heredity and variation, MENDEL's laws, JOHANNSEN's theory of pure lines, and the mutation theory, all enable the biologist to direct the inheritance of organisms. The investigator is now beginning to discern the presence of a law governing morphological processes. In the early XXth century knowledge of variation and heredity began to assume the character of a science, known as genetics. The study of the material basis of heredity, founded on a large accumulation of facts, constitutes an independent branch—cytology.

While plant breeding borrows the methods of genetics and cytology, applying them to the production of new varieties and forms, and to all the practical problems of plant and animal life, it also develops methods of its own. Thus breeding is entering upon a new phase, and is itself becoming a science. But, of course, even under modern conditions an element of art still survives and plays a not unimportant part. As in the past, the practical breeder sometimes makes notable discoveries. It should not be forgotten that the theory of breeding is born of practice and in turn extends practice. Such is the dialectics of knowledge, inseparably bound, as it is, with productivity. The interpenetration of theory and practice and their unity are fully borne out by the history of breeding as an art, a science, and a special branch of agriculture.

To the present day the breeding of both animals and plants is a concern of private firms. Hitherto in the U. S. A., England, France, Germany, Denmark, Spain, Italy, Japan and Argentina, new varieties have usually been produced by such undertakings. To the present day also in certain countries as, for example, France, private firms enjoy a monopoly of the production of new varieties, and even oppose the establishment of state breeding stations. The development of breeding, moreover, into a scientific discipline has been and is still being hindered by certain impediments as, for instance, advertising, freedom from control, and trade secrecy. Art has played and continues to play a dominant part in the breeding both of plants and animals. As a science, breeding is still in process of formation.

Yet glimpses of its entry upon this path are discernible even in the literature of the XVIIIth and the middle of the XIXth centuries. Here we need only mention the works of KOELREUTER, KNIGHT, GÄRTNER, NAUDIN, MENDEL,

RIMPAU and of DARWIN himself. But on the whole breeding only began to take the shape of a science in the XXth century when many breeding stations were established, breeding organized at places of higher education, and text books of breeding as well as scientific journals devoted to the subject appeared.

The publication of *Die Methoden der Pflanzenzüchtung in experimenteller Prüfung—Anleitung zur Getreidezüchtung auf wissenschaftlicher und praktischer Grundlage,* 1889, by VON RÜMKER was an event of historic importance. A revised edition of this work appeared in 1909 under the title of *Die Methoden der Pflanzenzüchtung.* Mention should also be made of the classical researches of NILSSON-EHLE at Svalöv, an account of which was published in German in 1909-1911 under the title of *Kreuzungsuntersuchungen an Hafer und Weizen.* The last three decades have been marked by the publication in five volumes of *Das Handbuch der landwirtschaftlichen Pflanzenzüchtung,* a collective work which, under the editorship of FRUWIRTH, the Austrian plant breeder, went into many editions. The first volume, devoted to a general study of plant breeding, appeared in 1900, and the seventh edition in 1930.

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Planned plant breeding by the state, upon which we have embarked, necessitates the formulation of a sound theoretical basis within the shortest possible time. While our socialist fatherland develops plant breeding on a large scale, plans and creates a network of breeding stations, mobilises large bodies of scientific workers, and introduces into breeding an increasing assortment of plants and animals, it is greatly interested in the promotion of breeding as a science. Only well-founded theory can enable us, as soon as possible, to achieve the modification of varieties according to the needs of socialist economy.

We do not reject the conception of breeding as an art, but to insure certainty, speed and preeminence in the essential tasks we need a well-worked out theory of practical breeding procedure. Scientific bodies cannot rely upon intuition merely hoping to achieve success by chance. A solid scientific foundation is needed so that work may be properly regulated and have a definite aim.

Of what does breeding as a science consist?—Many authors abroad and at home thought, and still think, that breeding is identical with genetics.

BATESON, who in 1906 introduced the word "genetics," defined its meaning in the twelfth edition of the Encyclopaedia Britannica, published in 1922. Genetics, he said, is the science of heredity and variation and the study of selection. In the Latin countries, as for instance, Italy, Spain, and all the South American states, plant breeding is called genetics and plant breeding stations are known as institutes of genetics. According to many authors plant breeding is the application of genetics to practical ends. The plant breeding text book written by D. F. JONES, the American plant breeder, is entitled: *Genetics in Plant and Animal Improvement.* In the opinion of many authors, breeding methods are based on genetic principles. A publication devoted to breeding in America is called the *Journal of Heredity.* The sub-title of the German publication, *Der Züchter,* describes it as a journal of theoretical and applied genetics. One of the most widely used text books on breeding in America, that written by BABCOCK and CLAUSEN, is called *Genetics in Relation to Agriculture.* Some authors consider that the word breeding should be replaced by the term "special genetics," by which is meant the genetics of particular species of plants and animals. By a historical process, the progress of scientific breeding, natural specialization and the development of branches directly associated with practical plant and animal breeding inevitably leads to the segregation of breeding as an independent science.

The basic principles of genetics embodied in the study of heredity and variation, as well as several principles of cytology, form one of the chief components of breeding, although they are not synonymous with it. The science of breeding is the study of producing varieties for human needs.

Genetics is paramountly concerned with the problems of genes, variation, heredity, sex, and questions of phenogenetics, both of plants and animals. As a theoretical science, it searches for appropriate material with which to experiment. Hence its preoccupation, both in the past and in the present, with the most convenient object for investigation, the *Drosophila* of classical experiments, with which the outstanding discoveries of modern genetics have been made.

As a science, the scope of breeding is defined by the necessity for obtaining practical results, for concentration upon the improvement of domesticated animals and crop plants, and for embracing every aspect of their biological, physiological, biochemical, and other characteristics, while at the same time devoting the greatest share of attention to the individuality of the particular object under investigation.

Since, in part, they treat of heredity and variation, certain parts of genetics and breeding interpenetrate. Breeding makes use of the laws of heredity discovered by genetics; genetics draws on the data of breeding in order to incorporate them into generalizations. In its earliest stages genetics is naturally bound up closely with breeding theory. The investigation of genetical and breeding problems, the marked advance of knowledge generally of the subject, the blossoming of genetics in the last decade consequent upon discoveries in cytology, and the extensive breeding activity which accompanied it, all tended to bring about its branching off into separate sciences, a development which the history of science shows is usual.

It must not be supposed because investigators work simultaneously both in breeding and genetics, and breeders require a knowledge of genetics, that these two spheres of discipline are of necessity inseparable. Their divergence has, in fact, become real enough in the course of research, and must be reckoned with both in theory and in practice.

Evolutionary principles permeate the whole science of breeding. In effect breeding is man's interference in the morphological formation of animals and plants; in other words *it is evolution directed by the will of man.*

The word selektsia ("breeding") derived from the Latin *seligere,* to select, or in a wider sense, to study selection, conveys as clearly as possible the nature of the scientific system called for. This word perhaps has a truer claim to universal recognition than, say, the French description "amélioration des plantes cultivées et du bétail," or the German word "Züchtung," which literally means breeding; rearing; growing; cultivation. The English term "plant or animal breeding," which is the equivalent of this German word, is no better. In many of the Latin countries, where research work is still in its earlier stages, breeding, as we have already mentioned, is translated by the word "genetics." To our way of thinking, the Russian word for breeding, that is the study of selection in the wider sense, defines with sufficient exactitude and embraces in its entirety, the general content of that system which we have in mind. The production of new varieties and "selection" involves more than variability and heredity. Selection necessitates the consideration of original material and of the physiological, biochemical, and other varietal differences as well as the complex process of segregation and creation of desired forms. The study of selection has acquired a wider meaning in the period that passed since Darwin

gave to his classic work the title *On the Origin of Species by Means of Natural Selection.*

In the general classification of science, breeding is related to biology and borders on many branches, borrowing something from each of them, particularly from genetics. The well known text book of animal breeding by KARL KRONACHER is entitled *Die Grundzüge der Züchtungsbiologie.* By virtue of its practical aims, its specific nature, and, above all, the demand made upon it for economic results, breeding is compelled to be a science in itself. Because of the extent of practical knowledge of the subject increasing from year to year and the exclusively practical value of it in pedigree animal and plant production, breeding has, of necessity, become a special department of knowledge. So vast is the scope of classified knowledge which constitutes the study of plant and animal breeding that it has to be treated separately as a special branch of science. Breeding has developed its own methods, the methods based upon the principle of pure lines and that of inbreeding.

According to our interpretation the science of plant breeding consists of the following sections:

1. The study of the potentials of original varieties, species, and breeds (the phytogeographical basis of breeding).

2. The study of inherited variability (laws governing variation, the study of mutations).

3. The study of the effect of environment on the emergence of varietal characters (variety and environment, the influence of particular factors of environment, the study of the stages of plant development and its application to breeding).

4. The theory of hybridisation of closely and remotely related forms.

5. The theory underlying breeding practice (self- and cross-pollination, vegetative and apogamous reproduction of plants).

6. The study of the chief aims of breeding: immunity from disease, certain physiological characters (winter-hardiness, resistance to drought, photoperiodism), properties useful for industrial purposes, and chemical composition.

7. Special breeding—breeding of particular crops.

Such, in outline, is the substance of the study of plant breeding. It will no doubt in the future be necessary to increase the number of sections.

The foregoing enumeration of the constituents of the science of breeding shows the relationship which it bears not only to genetics but also to systematics, geography of plants, biology of flowering, cytology, ecology, biochemistry, physiology, and technology.

As supplementary to the study of a general nature, the great importance of individuality of aim, of specificity, calls for investigation of the breeding of particular species of animals and plants.

In reality, breeding is a development of evolutionary studies. It provides an experimental basis for the evolutionary process. A bred variety is the result of man's interference with the nature of growth. Hence breeding is a significant link in evolution controlled by man. If DARWIN largely based his theory of evolution and natural selection on data provided by the practice of breeding as an art, more important still must become the practice of breeding as a science, indispensable for explaining the evolutionary process. Thus, in the course of their actual work research workers in breeding cannot avoid the problems of evolution. As the science of breeding progresses it will strengthen their control over the living organism, and will confer upon them a powerful

means for modifying the inherited constitutions of these living organisms according to their desires.

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Unlike the fundamental sciences such as chemistry, physiology, botany and zoology, *breeding, regarded as a scientific system is complex to a high degree:* it borrows from general science, methods and laws of plants and animals and subjects them to a detailed study appropriate to the aims of breeding down to the individual variety. In controlling heredity it relies wholly on the findings of genetics, cytology, and embryology, while in the study of breeding technique it depends upon the biology of flowering, physiology, chemistry, technology, phytopathology, entomology. But the definition of breeding as a science rests chiefly on the fact that because of its complexity it not merely selects certain parts of other sciences but transforms and differentiates them to an extent necessary for the achievement of its aim: the production of a new variety. On the basis of discipline it works out its own methods, and establishes a regular procedure which the formative process follows in the creation of new variety.

Because of its youthfulness as a science, and its dependence on other sciences, breeding is subject to change. It is still in process of formation—*in statu nascendi.* Yet in spite of this, it already has methods of its own; and some are peculiar to it such as those of the differential systematics of species, pure lines, and inbreeding. Many of the fundamental ideas of modern genetics have indeed been worked out by breeders as, for example, polymery and the inheritance of physiological characters.

If we take into account the considerable amount of potential knowledge on the subject, then breeding as we interpret it, the study of the control of the heredity of organisms, is a science in formation, a science of the future, thus differing from those sciences which are already fully formed.

The dependence of varieties on environment and the impossibility of divorcing them from it, requires that they be studied under certain definite conditions.

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The question of environment and the interaction of the organism and the environment is one of the most important branches of breeding.

Let us pause here to examine in some detail the main sections of breeding as regards their statics, *i.e.,* their condition at the present time, and the dynamics of the formation of the theory of breeding.

In order to control organisms when breeding, knowledge is particularly necessary of their individuality, of the species and breeding potentialities of the object under investigation, and of the ranges of morphological, physiological, quantitative and qualitative variations within the species itself. It is also necessary to know wherein lie the potentialities of the species, and what are the genetical relationships within a given group. A differential interpretation of species is called for, involving the application of modern methods, including those of cytology, anatomy, physiology, biochemistry, embryology, and pathology. *The study of original material,* and of the origin of cultivated plants, are fundamental requisites of the science of breeding.

While in the botany and plant systematics sections these requisites are of an entirely general character, in breeding they have a definite and special content. It is not accidental that in regard to such sections breeders are applying methods similar to those of differential systematics and the geography of plants. In this sphere there is abundant scope for work of such importance as would serve even the highest aims of the plant breeder. As a rule, in the

past, he dealt with parts of species; the near future holds promise of a synthesis of scientific knowledge that will throw light on the range of variation within the species, the systematics of species, the extreme variants, and the range of physiological, chemical, and other properties. As a result of the investigation which we have begun along these lines in recent years, it has been clearly demonstrated that the old ideas which were concerned with fragments of species and the incidental material with which breeders worked, must be changed at the root. *From now on the basis of scientific breeding should consist of phytogeographical information relating to varietal potentialities of species and breeds.*

Such a basis, together with the application of the differential method, would provide a starting point for breeding investigations.

The second section is the study of variation, while the third section deals with *the interrelationships of the environment and heredity of the organism and external conditions* or, to be more precise, the study of the genotype and phenotype, according to the theories of JOHANNSEN. This section is concerned with the study of mutations and their application to breeding, of the laws and inheritance of variability, of quantitative and qualitative characters, and of the range of variation. The distinction in principle between the gene and outward character has already been made clear by modern genetics. Yet in the past breeders did not allow for modifications of the phenotype by environment. They did not reckon with the possibility of imminent great changes in environment resulting from extensive use of chemical fertilizers, irrigation, and vernalization. The last mentioned, vernalization, might radically alter the phenotype even to the extent of changing perennials into annuals, and late varieties to early, with corresponding modifications of characters.

Outstanding importance has become attached to the study of the influence of individual factors and combinations of factors on separate stages of development, both of individual plants and different varieties. Variety physiology should be studied in the near future.

The fourth section consists of the theory of hybridization, which has been brilliantly expounded on the basis of MENDEL's laws and MORGAN's chromosome theory of heredity.

In this section the science of breeding is especially near to genetics. It borrows largely from genetics, which has itself been very largely worked out by breeders. In regard to breeding the theory of hybridization should be rendered more amenable to practical application than is possible in a general course of genetics. It should be emphasized that breeding should pay particular attention to quantitative, physiological, and economic characters. As a science of the future, it should also embrace a complete study of pairing, in other words, of the correct choice of components for crossing. So far this branch has been hardly touched by modern genetics. The theory of hybridization should place at the disposal of the breeder formulae more directly applicable than any hitherto known, but it will only be able to do so after a large planned investigation of a variety of subjects, both analytical and synthetical, has been undertaken. Hitherto, to a large extent the breeder has paired fortuitously.

Not less thoroughly, having in view as a definite aim the creation of economically useful varieties, the study of interspecific and intergeneric hybridization should be carried out.

The next section is called *the theory underlying breeding practice:* it is concerned with the study of the principles involved in working with various types of plants: self-pollinating, cross-pollinating, intermediate, and others. This section includes systematized information on the biology of flowering and fruit formation. Thus it deals with the most important aspects of plant breeding.

The chief cultivated plants should be studied in the near future in regard to flowering, apogamy, and the manifestation of self-sterility and self-fertility. Included in this study is a wide range of ecological-geographical material, and also the diversity of biological types to be found within one and the same species.

It is essential that all these sections, the general outlines of which are touched upon by botany and biology, be differentiated with regard to the breeding of various groups of plants.

A theoretical elaboration of the method of inbreeding is particularly necessary, both by producing new forms as a result of the propagation of close relatives and the creating, within the shortest possible time, of true breeding types of cross-pollinating plants. This section throughout calls for investigation, by means of experiment.

The sixth section consists of the study of breeding with specific aims in view: chemical composition, properties desirable for industrial purposes, physiological properties, and immunity from disease.

This section is intimately bound up with physiology, biochemistry, technology, phytopathology, and entomology.

In spite of its exceptional importance to breeding, which is inseparable from economic needs, it has so far been little studied.

Having enumerated the foregoing branches, we should next consider the range of varietal diversity within the species under investigation, and determine the breeding possibilities of the chief characters such as, for instance, resistance to drought and cold, and chemical composition in its effect both on quantity and quality. It is particularly necessary to demonstrate the laws governing the manifestation of variation in these characters. When studying the process of segregation in hybridization, special attention should be paid to the range of differences which show themselves in certain characters.

The knowledge which exists in regard to some items of this section is so scattered and inadequate as to preclude the formation of anything like a sound theory. Ahead lies colossal labor in the spheres of the biochemistry, physiology, and technology of varieties.

Such spheres, bound up as they are with breeding, will no doubt provide the main branches of the science with facts of exceptional value. A differential knowledge of varieties will afford a real insight into the physiological and biochemical aspects of plants. Equally certain is it that cooperative work on the part of physiologists, biochemists, and breeders will enrich physiology and biochemistry. An example of this cooperation was the discovery of vernalization—one of the most powerful instruments of modern plant physiology—made during work on varieties at a plant breeding station.

In the near future we shall no doubt be able to perceive system and regularity where hitherto there has been chaos and obscurity. At the present time, as a result of the mutual exchange of methods, very fruitful work is being done at the points of contact between different sciences, on the borderline between spheres of knowledge. Some of the chief biological investigations, extending over a period from Darwin's theory of evolution to the mutation theory of de Vries, have been rendered possible by freely drawing upon data made available by plant breeding.

A distinguishing feature of the science of plant breeding is its complex approach to the plant, involving various methods of investigation. Furthermore, physiology, biochemistry, and technology are closely connected with plant breeding, which is not only a science, an evaluator of varieties, but something more, a means of revealing the differential of species of the chief crop plants in order

to demonstrate laws governing the morphological formation of the chief physical and chemical characters.

The connection between breeding on the one hand and genetics, physiology, ecology, biochemistry, systematics, and plant geography on the other, reveals new, peculiar, and specific aspects of these sciences. By incorporating their tried methods breeding endows such sciences with new content.

To a certain extent breeding is to genetics and other sciences what medicine and technology are respectively to biological and physico-chemical sciences.

Special breeding, that is the breeding of particular plants, consists of the study of the individuality of the plant, its differential systematics and geography, its biology of flowering and fruit formation, and its ranges of variation in all the chief characters. In order to comprehend his material, the breeder should study it in its historical and geographical relationships, and should seek to explain the differentiation of the most important characters in their interaction with environment. Knowledge must be obtained of the specific characters of the plant and the applicability of various methods of breeding. We would not be justified in regarding this section as equivalent to special genetics or, in particular, to modern genetics which is based on the study of an insignificant number of characters in only a few varieties. It should be based wholly on phytogeographical differential knowledge, due consideration being given to physiological, chemical, and technical characters of varieties, their immunity or susceptibility to disease, and their reactions to environment at the various stages of their development.

Such approximately is the outline of what constitutes the science of plant breeding, according to our understanding at the present time. The scope of the real knowledge, of which the study of the subject consists, is sufficiently wide to justify specialization. Already breeding has its own methods. A host of examples of variability within varieties, morphological, biochemical and physiological may now be reduced to order and systematized. As a consequence of all these considerations, it is permissible to segregate breeding as a special science.

It is not a question of status; the essence of the segregation of plant breeding as a science in itself lies in the fact that it was raised to a new level by the formulation and crystallization of knowledge which increased its powerfulness as a weapon in the struggle against nature, and enabled the plant breeder more actively to participate in the great work of socialist construction.

The working out of plant breeding theory will doubtless necessitate the addition of new sections, and its development will inevitably lead to that of other biological and agricultural sciences. A great amount of collective effort, organized according to a definite plan, will be needed in order to render more concrete the sections and chapters enumerated. The progress of practical plant breeding during the last thirty years provided the stimulus for bringing about its separation into a science on its own account, but that achievement is not sufficient.

The need for scientific discipline in plant breeding has never been so acute as it is in our country, with its socialist structure designed for clearly defined aims, its unlimited horizon of work and its enormous body of research workers. Only a maximal, concrete productive theory will suffice for the strong organization which has been built up, and still continues to develop, in connection with our plant breeding activity. The large number of plants with which we have dealt and on which breeding work is proceeding, calls for differential knowledge. But at the same time and to no less extent, the general synthetic study of breeding and the dialectical unity of theory and practice, especially

under conditions of socialist economy, necessitates that the Soviet state shall call upon breeders to meet in the shortest possible time the chief needs of variety seed and pedigree livestock production, and provide the prerequisites for the creation of a sound theory.

The vast scale on which breeding is conducted, its industrialization, its need to conform to the requirements of socialist industry, all demand the formulation of such a theory. At the same time the vast scale of the work which it is doing provides unique opportunities for harmonizing theories in the course of experience and observation.

We are interested in the study of underlying principles of all aspects of general genetics: the problems of the gene, the theory of mutation, the theory of hybridization, and the problems of genetics. We are persuaded that more thorough research will afford fresh stimulus to breeding. On the strength of this conviction, laboratories for the study of genetics are being established at our breeding stations. At the same time general genetics will itself derive a strong stimulus from the practical work of breeding. That such a promise will be fulfilled is shown by the history of the theory of evolution—of genetics itself. Within the shortest possible period the science of breeding must advance through a whole series of upward stages to a level immeasurably higher than that on which it rests today. Only by working out a theory of breeding will the investigator be able to achieve real control over the organism—the ultimate aim of modern biology.

PHYTOGEOGRAPHIC BASIS

of

PLANT BREEDING

1. **Local Varieties and Their Significance:**— The varieties of cultivated plants grown in the different regions of the Soviet Union until recently were varieties introduced from various localities and countries, and were inseparable from human migration and colonization. The list of cultivated plants reflects the history of our country in its recent past, it shows the effects of individual peasant farming. In the separate groups and varieties of plants one can trace the routes by which they were brought from Western Europe, the United States, Asia Minor, Mongolia, and Iran. In the pre-revolutionary period, the introduction of new varieties in our country was haphazard. Beginning with the eighteenth century, individual amateur growers and societies unsystematically introduced new varieties from abroad. Sometimes these new varieties were quite valuable but because of the vastness of our country and the complete absence of any state-planned system of plant introduction, the imported varieties usually restricted themselves to very limited areas and disappeared.

It may be considered that pedigree seed production, in the real meaning of the term, did not exist in our country before the October Revolution. We have just begun a planned distribution of varieties in accordance with the need of our large-scale socialized and mechanized agricultural economy.

Yet, there is no doubt that the varietal materials which were introduced in our country and cultivated for decades and centuries were subjected to natural selection, and also to deliberate or casual artificial selection, and that some local varieties evolved that were ecologically adapted.

The proximity of the Soviet Union to the basic centers of origin of numerous cultivated plants facilitated the selection of exceptionally valuable forms. Certain crops such as fiber flax, and some varieties of wheat, rye, clover, and timothy, are represented in our country by excellent local varieties. Our investigations on flax, for instance, have shown that the northern varieties of fiber flax found in the European part of the Soviet Union occupy first place among the varieties of the world. The local Middle Eastern and Transcaucasian varieties of wheat, barley, forage grasses, grapes, and fruit trees consist of valuable original adapted forms which will require great care in breeding in order to retain all the valuable properties they already possess.

The concept of "local variety" is actually very relative; it usually embraces both old varieties which had undergone natural selection during decades and even centuries, and accidental varieties which have been but recently introduced and which have lost their original character, original names, and pedigrees. A great many of the so-called local varieties come within this category.

In appraising local material for breeding purposes, a very important factor is the presence or absence of a diversity of hereditary forms. In this respect different plants and varieties, grown in different environments, vary greatly. Under some conditions the local assortment is represented by heterogeneous populations consisting of many forms differing from one another morphologically and physiologically. In other cases, the local varieties consist of populations of uniform physiological and morphological characters. When, as frequently occurs in Transcaucasia and in central Asia, the local materials are heterogeneous, they afford the greatest possibilities for breeding. For example, plantings of millet in southeast European Russia consist of heterogeneous populations ranging up to a dozen botanical varieties. Yet, frequently the so-called local varieties are very uniform, having resulted from

uniform varieties which were introduced from other parts of SSSR or abroad some time previously and which have lost their names.

It is natural that the first step in breeding should be the *maximum utilization of local materials,* the segregation of their most productive and valuable forms. The success of breeding in our country in recent years has been chiefly based on this segregation of the most valuable forms from local populations. Our best varieties of winter and spring wheat, rye, flax, and barley, produced in recent years by our breeding stations, are chiefly the result of selection from local varieties. In their work with old crops the newly established breeding stations must first of all devote their attention to the investigation and the utilization of local varieties.

In beginning practical breeding work it is paramount to become well acquainted with the potentialities of local materials. These should serve as a starting point for the subsequent improvement of varieties. In all breeding stations, there should be special seed plots for the preservation of all valuable local materials.

2. **The Significance of Material Introduced from Abroad or Brought from Other Regions of SSSR:**— However, the procedure is very different when the problem concerns the breeding of new varieties for a region where the crop in question has not been previously cultivated. In this case, attention should be concentrated on securing the most interesting and valuable materials to work upon.

It can be emphasized that all the achievements of Canada and of the United States in their great expansion of the cultivated areas of wheat, barley, oats, rye, forage, and fruit crops are based on an introduction of suitable varieties from our country, from India, and from Western Europe. The winter wheat grown in the dry regions of the United States is the product of varieties imported from our southern regions. In recent years the greatest progress has been made in the United States, Canada, and Argentina by crossing very distant geographic races introduced from Europe, India, and China. The success of noted breeders, such as I. V. Michurin, Burbank, and Hansen, is chiefly based upon their use, in crossing, of extensive varietal materials from foreign countries. The history of breeding clearly shows that the great achievements of the past decade have resulted from the use of breeding materials introduced from distant regions. This can most easily be seen in the cases of Canada, the United States, Australia, Argentina, and South Africa, which acquired all their breeding materials from other countries, but this was also true of countries that also had their own valuable local materials. Sweden, for instance, has greatly improved her local wheat varieties by crossing them with the English "Squareheads." This is also true of France. Germany, in the last decade, has introduced breeding materials from many countries, for which purpose special expeditions were sent to Asia Minor, South America, Afghanistan, and India.

It is difficult to imagine our existence today without such crops as the sunflower, corn, potato, tobacco, and Upland cotton, all of which were imported not long ago from America. In relation to new crops, special attention should be given to a well planned system of plant introduction, because the success or failure of new crops is inseparably bound up with the varieties originally chosen.

The new conditions created by the socialization and mechanization of our agriculture have put new qualitative demands upon our plant varieties such as resistance to shattering of the mature grain, resistance to lodging, and

adaptability to mechanized harvesting. Our local varieties have to be revaluated in accordance with the new demands.

Moreover, however valuable our local varieties are ecologically, they are yet far from ideal. The spring wheat varieties of the regions of Volga, Ukraine, and western Siberia which have undergone centuries of natural selection still suffer from drought.

The winter wheat varieties, even in the chief regions of cultivation, often are killed in cold winters.

Thus, the necessity of a radical change in varieties to correspond with the conditions of our rigorous continental climate, and the new demands of our socialized agricultural economy, makes it of utmost importance to make the widest possible choice of new breeding materials.

The importance of plant introduction is especially great for our subtropical regions where all efforts should be directed at bringing in suitable assortments of plant varieties from abroad.

3. **The Theory of Plant Introduction:**— Investigations conducted in recent years by the All-Union Institute of Plant Husbandry have demonstrated a number of principles governing the geographic distribution of the plant resources of the earth, and have greatly helped in pointing out the direction of search for new plants, new species, new varieties.

The botanical study of the globe is still far from complete. Botanists probably are acquainted with not more than half of all species of flowering plants in existence. The vast continents of South America and Africa, India, China, Indo-China, and Western Asia have been studied but little. There still exist many regions where botanists have never set foot. According to our most competent taxonomists, there remain to be discovered hundreds of new species in our own republics of Transcaucasia and Central Asia.

But from the incomplete data which we now possess on the vegetation of the earth, the important fact of the geographic localization of the process of species formation has been made clear. The geography of plants shows definitely that in modern times *the distribution of plant species on the earth is not uniform.* There are a number of regions which possess exceptionally large numbers of varieties. Southeastern China, Indo-China, India, the Malay Archipelago, southwestern Asia, tropical Africa, the Cape regions, Abyssinia, Central America, South America, southern Mexico, countries along the shores of the Mediterranean, and the Near East possess extraordinary concentrations of plant varieties. On the other hand, the northern countries—Siberia, all of central and northern Europe and North America—are characterized by a poverty of varieties.

Central Asia is surprisingly rich in varieties. Within the Soviet Union, from Crimea towards Transcaucasia and the mountainous regions of Central Asia through Altai and Tian-Shan, the number of varieties markedly increases. It reaches its peak in the Caucasus and the mountains and foothills of Central Asia. Here the number of species is very great for a given area. The concentration of species in these regions is ten times greater than in Central Europe and still greater when compared with the northern regions.

In some parts of the world, the concentration of varieties is remarkable. Thus, for example, the small republics of Central America, Costa Rica and Salvador, have areas about one hundredth of that of the United States, yet they possess a number of species as great as is found in all of North America, i.e., in the United States, Canada, and Alaska combined.

In an interesting new paper, entitled "The Analysis of the Flora of Caucasus," Prof. A. A. GROSSHEIM has for the first time indicated exactly the regions of Transcaucasia which possess the greatest diversity of species.

In searching for new useful plant species, both here and abroad, one should keep in mind the locations which possess the greatest wealth of species and pay special attention to these locations. Thus, for instance, in spite of numerous expeditions in search for it throughout Central Asia and Kazakstan, the famous rubber plant, Tau-saghyz, has been found only on the mountain range of Kara-Tau in Kazakstan, a locality which possesses a rich endemic flora. Another remarkable rubber plant, Kok-saghyz, was found along the Chinese frontier, on Tian-Shan, which also has a rich variety of species. Krym-saghyz is found in Crimea and originated in Mediterranean countries which have an exceptionally rich flora.

Our investigations of recent years have clearly revealed the locations or, as we prefer to call them, the centers of species formation, of the most important cultivated plants of our present time. We have naturally directed most of our research toward the varietal resources of those crop plants which are most important to our country.

Within the past decade, in accordance with a unified plan, the Institute of Plant Industry has conducted extensive and systematic geographical investigations of a great number of species of crop plants. These investigations have been primarily concerned with field, vegetable, and fruit crops and their wild relatives. Our attention has been concentrated on the *intraspecific composition of particular plants* and on the botanical study of the varietal composition of certain Linnaean species.

The study of several hundred cultivated crops conducted by a large body of scientific workers has led us to a conception of the Linnaean species including the cultivated plants, as a definite *heterogeneous system.* As we interpret it, *the species represents a more or less distinct heterogeneous and variable morpho-physiological system, the origin of which is associated with a particular environment and area.*

The study of several hundred species showed an absence of monotypic species, *i.e.*, those consisting of only one definite race or one distinct botanical form. All species were found to be composed of large or small numbers of hereditary forms ("Jordanons" and genotypes).

A detailed study of variability within species showed from the very outset an underlying principle, manifested in a striking *parallelism* in the heritable variability of closely related genera and species—a resemblance between many hereditary forms representative of them. This fundamental law we have called the *law of homologous series in inherited variation.* The formulation of this law gave an impetus to all our research work on varieties, because it showed numerous missing links in the taxonomic systems of cultivated plants and their related wild forms. Theoretically, these links must either exist in the present or have existed in the past. The question naturally arises: *in what regions must one seek for these absent links?* Thus we have come back to the old problem of the origin of cultivated plants, but with new and definite aims. The solution of the problem of origin of cultivated plants is in mastering the genetic potentialities of cultivated plants.

It has become clear to us that botanists knew very little about cultivated plants. As we went deeper into the study of heritable variability, new possibilities of varietal forms continued to open before us. The question arose: *what are the varietal plant resources of the world?*

During the last ten years the Institute of Plant Industry, proceeding on a definite plan, has conducted a large number of expeditions both within the limits of the Soviet Union and abroad.

The location of the principal geographic centers of origin or formation of cultivated plants was established by us with the aid of the differential phytogeographic method. It consists of the following:

1. A strict classification of the plants studied into Linnaean species and genetic groups based on systematics, morphology, genetics, cytology, and immunology.

2. The location of the original areas occupied by these species in the past, when communications were more difficult than at present.

3. A detailed determination of the composition of botanical varieties and races of each species, or of the general system of hereditary variation within species.

4. Determining the regions and countries wherein occur the heritable forms of a given species and the geographic centers where the basic varieties are concentrated. As a rule, in the original centers are found numerous endemic varietal characters. In cases when the endemicity of a given group is of ancient origin (paleo-endemicity), it may embrace not only characters of species and varieties but also those of whole genera of cultivated plants. This is often the case.

5. In order to establish more exactly the centers of origin and initial formation of varietal forms, it is also necessary to determine the geographic centers of origin of varieties of closely related wild and cultivated plants.

6. The original centers often contain a large number of genetically dominant characters. In the general scheme, as shown by a study of the geography of cultivated plants, recessive forms, resulting from inbreeding and mutation, are found mostly at the periphery of the ancient basic areas of the cultivated plant species and also in isolated regions (on islands and in mountainous regions).

7. Finally, a confirmation of the phyto-geographic differential method may be found in archeological, historical, and linguistic data, but, on the whole, these data are too general for practical needs which require a concrete and exact knowledge of species and varieties.

It is essential to differentiate between primary and secondary centers of varietal origin. Cases are known in which the present large number of varieties comprising a species is the result of a union of two or more species or of their hybridization. For instance, Spain contains an exceptionally large number of varieties and species of wheat—due to the general geographic location, the mountains, and the history of this country. However, the total number of forms actually means very little because, as shown by direct analysis, the number of subspecies *within the limits of separate species* found in Spain is very small compared to the number found in the real centers of initial formation of these species. The great variety of wheats in Spain is explained by the introduction of many species from different centers.

The application of this complex method naturally has required the collection of enormous quantities of material, and knowledge from all parts of the world. But as a result, we have data concerning the potentialities of the morphological and physiological properties within species which are indispensable for breeding work and genetic studies; it also gives us a sound approach to the knowledge of the dynamics of the evolutionary process.

Genetic investigations have shown that external uniformity sometimes conceals a great variety of genetic potentials. For instance, in crossing the relatively uniform Afghan Mountain peas with the extremely recessive cultivated European varieties it was found that under the external uniformity of the original Afghan varieties there was hidden a great number of genes which, after hybridization with the extreme European recessives, brought out the diversity of cultivated forms (L. I. Govorov).

Natural mutations and hybridization in secondary centers of origin may give rise to new forms which are often of great practical interest to the plant breeder. In our work with flax, for instance, we discovered that at the periphery of the area of origin of flax there separated out forms of special practical importance to the breeder because of the height of the plants, the type of branching, and the quantity of fiber. The winter-hardy wheat varieties are to be found, for the most part, not in the primary endemic areas but at the limits of cultivation, in high mountainous regions, or in the north. In some cases, as shown by genetic research, this fact is connected with the recessive nature of the character of winterhardiness in many varieties. Of exceptional interest are new recessive forms of waxy corn and waxy beans which have arisen in China after these American plants were transplanted from the New World to the Old.

Finally, of great importance is *the use, for parental materials, of the new hybrid forms created by the plant breeders of the world.* While utilizing material found in the basic primary centers which contain an enormous reserve of new and valuable genes, it is at the same time necessary to make the fullest possible use of materials found at the peripheries of plant cultivation, especially the products of the latest breeding in various countries.

The large amount of work performed during recent years in the Soviet Union by the collective efforts of the Institute of Plant Industry in the comprehensive study of the varietal resources of the world for the most important economic plants, based on the colossal amount of newly-collected materials, has fundamentally changed our conceptions of the varieties and species composing our economic plants. Even in such crops as wheat, potato, corn, legumes, rye, and flax, which have been bred for decades, we found enormous untouched varietal resources in the primary centers of their origin, in ancient agricultural regions in the mountainous sections of central and South America, southern Asia, and Abyssinia. Soviet scientists have discovered almost one-half of the new species of the most important cultivated plants and a great number of new varieties previously unknown to science. In the case of certain plants such as the potato, the newly discovered species and varieties literally revolutionized our conception of the source materials.[1]

In wheat, we have rediscovered three-fourths of the new botanical varieties and half of the new species. An exceptional wealth of genes has been discovered in wheat and in barley growing in Abyssinia, in the tiny area devoted there to agriculture. Here is concentrated a remarkable diversity of varieties of this, the most important bread grain of the earth. An enormous number of new varieties of wheat and other crops have been discovered in Afghanistan, Turkey, and northwest India.

We have located the regions of maximum concentration of primary diversity for the species and varieties of cultivated plants. It was ascertained that a considerable number of the cultivated plant species had remained within

[1] See S. M. Bukasov: [Revolution in the breeding of the potato.] All-Union Institute of Plant Industry, Leningrad, 1933.

the confines of this ancient primary center of origin. Dozens and even hundreds of species of cultivated plants are still indigenous to the regions where they had first been cultivated and where they had remained undisturbed by European explorers until the present time. This localization is especially striking in Central and South America where the primary centers of origin of economic plants are very restricted in area. It is also true of southern Asia. One of the most interesting regions of origin of forms and species of wheat and rye and particularly of fruits is our Transcaucasia and the adjacent regions of northwest Iran and northeast Turkey.

Here the process of *species formation* in such plants as wheat, alfalfa, pear, almond, and pomegranate is strikingly in evidence. It seems that one can trace here, *in statu nascendi,* the process of segregation of species and of larger genetic groups of these plants.

We have even succeeded in locating accurately the basic areas of origin of the primary species for such plants as wheat, barley, corn, and cotton, plants which have long since been distributed far and wide over all continents.

We have defined, with comparative exactness, the locations of the primary regions, which we have called the *centers of origin* of the species and variety potentials for several hundreds of plants, including all those of economic importance (but excluding ornamentals and park plants). In these regions are often found the closely related wild species of the plant in question, but not invariably. For some plants, such as corn, no original wild species have yet been discovered.

Our early efforts were to study the more difficult plants, such as wheat, rye, barley, corn, and cotton, which are at present widely cultivated throughout the world, and which have long since spread beyond the centers where they were first cultivated. For such plants, it would be superficial to consider only the area for the entire species, not including the varieties and types of which they are composed. In order to solve the question of location of their origin, it is necessary to employ the differential geographic method which has already brought to light a great quantity of new varieties and new characters, and the discovery of new species of wheat. Of these new species many were found to be localized within very narrow confines and were first discovered by Soviet expeditions to Abyssinia, Armenia, Georgia (SSSR), and Turkey.

With the study of new plants we often discovered *coincidences in areas of origin for many species and even genera.* In a number of cases we have found identical areas for dozens of species. Our geographic studies have demonstrated entire independent cultivated floras indigenous to certain regions.

4. **World Centers of Origin of the Most Important Cultivated Plants:**— In summarizing the work of the numerous expeditions conducted by the Soviet plant investigators in Asia, Africa, southern Europe, and North and South America, including a total of 60 countries and the entire Soviet Union, together with the detailed comparative study of enormous amounts of material of new species and varieties, we have located *eight independent centers of origin* of the world's most important cultivated plants. The task is not yet finished; we still know too little about southeastern Asia and we need to make a number of additional expeditions to China, Indo-China, and India in order to locate more exactly the centers of primary origin of cultivated plants and to obtain new materials. However, we can speak, with a degree of exactness that was unthinkable ten years ago, of eight ancient main centers of origin of world agriculture or, more exactly, of eight independent regions where various plants were first cultivated. In our earlier works we had limited ourselves to

defining centers of original agriculture, using but a few chief plants as indicators. We then lacked data for a comprehensive study of the subject. In the present work we have attempted to give as complete an enumeration as possible of cultivated plants indigenous in the different centers of origin. We have been compelled to make some important corrections in and additions to our original enumeration which was first formulated in our book "Centers of Origin of Cultivated Plants," published in 1926. Most of the expeditions and the largest amount of work on the study of the world's plant resources have been accomplished between the years 1923-1933. We shall now consider the separate centers of origin.

I. *The Chinese Center of Origin of Cultivated Plants.— The earliest and largest independent center of the world's agriculture and of the origin of cultivated plants consists of the mountainous regions of central and western China, together with the adjacent lowlands.* The following is a list of the chief endemic plants of this center, with the exception of ornamentals.[2]

CEREALS AND OTHER GRAINS :—

1. *Panicum miliaceum* L.—Broomcorn millet.
2. *Panicum italicum* L.—Italian millet
3. *Panicum frumentaceum* Fr. and Sav.—Japanese barnyard millet.
4. *Andropogon sorghum* Brot.—Kaoliang.
5. *Avena nuda* L.—Naked oats of large size. (Secondary center of origin).
6. A group of endemic hull-less, awnless barley varieties—(*Hordeum hexastichum* L.).
7. Groups of waxy maize varieties, *Zea mays* L.—(Secondary center of origin—typical recessive forms).
8. *Fagopyrum esculentum* Moench.—Buckwheat.
9. *Fagopyrum tataricum* Gaertn.—Tartar buckwheat.
10. *Glycine hispida* Maxim—Soybean.
11. *Phaseolus angularis* Wight.—Adzuki bean.
12. *Phaseolus vulgaris* L.—Bean. (Recessive form; secondary center).
13. *Vigna sinensis* Endl. subsp *sesquipedalis* Piper—Cowpea. (Secondary center).
14. *Stizolobium hassjoo* Piper and Tracy—Velvet bean. (Eastern Asia and Japan).

BAMBOOS :—

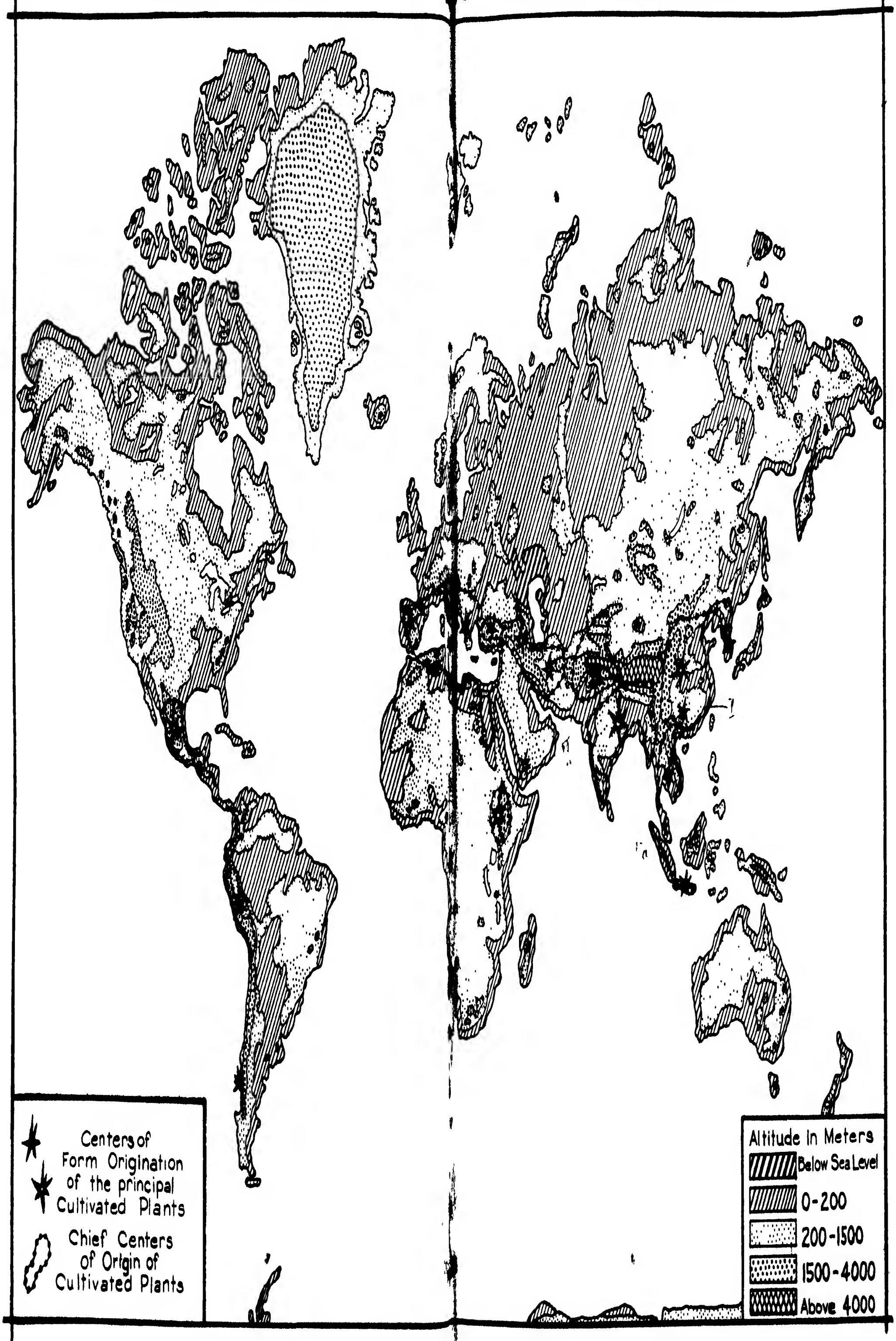
15. *Phyllostachys puberula* Munro, *P. quilioi* A. and C. Riv., *P. bambusoides* Sieb. and Zucc, *P. edulis* A and C. Riv., *P. nigra* Munro var. *Hononis* Makino, *P. reticulata* C. Koch, *P. mitis* A. and C. Riv. (this species is most frequently used as food), and other species.
16. *Arundinaria simonii* Riv., *A. nitida* Fr. Mitf., and other species.
17. *Bambusa mitis* Poir., *B. vulgaris* Schrad., *B. multiplex* (Lour.) Roensch, *B. spinosa* Roxb., *B. senanensis* Franch. and Sav., and other species.

THICKENED TAPROOTS, ROOT TUBERS, BULBS, AND AQUATIC PLANTS USED AS FOOD :—

18. *Dioscorea batatas* Decne, *D. japonica* Thunb.—Chinese yam.
19. *Stachys sieboldi* Mig.—Chinese artichoke.
20. *Raphanus sativus* L. *raphanistroides* (Makino) Sinsk.—Radish. Wild and cultivated in enormous diversity of forms.
21. *Brassica rapa* L. *rapifera* Metzg.—Separate geographic group of East-Asiastic turnips (Secondary center: Japan and the humid eastern China).
22. *Brassica napiformis* Bailey.
23. *Wasabia japonica* Matsum.—Japanese horse-radish.
24. *Arctium lappa* L.—Edible burdock.
25. *Amorphophallus konjak* K. Koch—Konyak. (Found chiefly in Japan).
26. *Petasites japonicus* Mig.—Butterbur. (Found chiefly in Japan).

[2] These lists of plant species are based mostly on personal investigations and trips and on the differential study of many cultivated plants conducted in the last ten years by the scientific staff of the All-Union Institute of Plant Industry. (See *Trudi po Prikl. Bot., Genet. i Selekts.*, volumes 11-27 and subsequent volumes, also supplements to them (1923-1934). For the tropical crops of India, China, and the Islands we referred to: WATT, Dictionary of Economic Plants; OCHSE, WILSON, TANAKA, AKEMINE and various monographs of the different genera.

WORLD CENTERS OF ORIGIN OF CULTIVATED PLANTS



— Figure 8 —

27. *Adenophora latifolia* Fisch., *A. verticillata* Fisch.—Ladybell (Japan).
28. *Eleocharis tuberosa* Schult. (*Scirpus tuberosus* Roxb.)—Water chestnut.
29. *Nelumbo nucifera* Gaertn. Lotus (possibly also in India).
30. *Sagittaria sagittifolia* L. var. *sinensis* Makino.—Arrowhead.
31. *Zizania latifolia* Turcz.—Wild rice. (The bases of stems and the leaf sheaths which are affected with smut are used as food).
32. *Ipomoea aquatica* Forsk.—Morning glory.
33. *Trapa bicornis* L. and *T. bispinosa* Roxb.—Water chestnut.
34. *Colocasia antiquorum* Schott.—Taro. (Wild and many cultivated forms). Possibly also found in India and the Sunda Islands.
35. *Lilium tigrinum* Ker., *L. Maximowiczii* Regel, and other species with edible bulbs.
36. *Elatostema umbellatum* Blume var. *convolucratum* Makino.

VEGETABLES :—

37. *Brassica chinensis* L.—Pak-Choi.
38. *Brassica pekinensis* Rupr.—Pe-Tsai.
39. *Brassica alboglabra* Bailey
40. *Brassica nipposinica* Bailey
41. *Brassica narinosa* Bailey

(37–41: Japan and eastern China).

42. *Brassica juncea* Czern.—Leaf mustard. (Secondary center of origin).
43. *Peucedanum japonicum* Thunb.
44. *Aralia cordata* Thunb.—Udo. (Found chiefly in Japan).
45. *Rheum palmatum* L.—Rhubarb.
46. *Allium chinense* Don. (*A. odorum* L.)—Chinese perennial onion.
47. *Allium fistulosum* L.—Spanish onion.
48. *Allium macrostemon* Bge.—(Northern China).
49. *Allium pekinense* Prokh.—In Korea and Japan. (Known only in the cultivated state, resembles *A. sativum* L.).
50. *Lactuca* sp.—Stem lettuce.
51. *Solanum melongena* L.—Eggplant. (A special form with small fruits).
52. *Cucumis chinensis* Pang.
53. *Cucumis sativus* L.—A large-fruited cucumber.
54. *Luffa cylindrica* M. Roem.—(Used as a vegetable and also for sponges).
55. *Cucurbita moschata* var. *Toonasa* Makino (var. *japonica* Zhit.)—A small warty squash. (Secondary center)
56. *Actinostema paniculatum* Maxim.
57. *Chrysanthemum coronarium* L.—Chrysanthemum. (Leaves are used as food); *C. morifolium* Ram. v. *sinense* Makino. (Petals are used as food).
58. *Perilla ocymoides* L., *P. arguta* Benth.
59. *Asparagus lucidus* Lindl.—Tuberous asparagus (Japan).
60. *Basella cordifolia* Lam.—Chinese spinach. (Possibly introduced from India).

CULTIVATED FRUITS :—

Group of the temperate zone

61. *Pyrus serotina* Rehd.—Chinese pear.
62. *Pyrus ussuriensis* Maxim.—Ussurian pear.
63. *Malus asiatica* Nakai—Chinese apple.
64. *Prunus persica* L., *P. Davidiana* Franch.—Peach. (The second species is a wild one).
65. *Prunus armeniaca* L.—Apricot.
66. *Prunus mume* Sieb. and Zucc.—Japanese apricot.
67. *Prunus salicina* Lindl. (*P. triflora* Roxb.)—Japanese plum.
68. *Prunus simonii* Carr.—Chinese plum.
69. *Prunus tomentosa* Thunb.—Chinese cherry.
70. *Prunus pseudocerasus* Lindl.—Cherry.
71. *Prunus pauciflora* Bge.
72. *Crataegus pinnatifida* Bge.—Hawthorn.
73. *Chaenomeles lagenaria* Koidz.—Chinese quince.
74. *Chaenomeles sinensis* Koehne, *Ch. japonica* Lindl.—Chinese quince, dwarf Japanese quince.
75. *Eleagnus multiflora* Thunb. var. *hortensis* Maxim., *E. umbellata* Thunb., *E. pungens* Thunb., and other species.
76. *Zizyphus vulgaris* Lam. (*Z. sativa* Gaertn.).—Chinese or common jujube.
77. *Hovenia dulcis* Thunb.—Japanese raisin tree. (The sweet fruit stalks are used as food).
78. *Ginkgo biloba* L.—Ginkgo.

79. *Juglans sinensis* Dode, *J. sieboldiana* Maxim., and other species.—Walnut.
80. *Carya cathayensis* Sarg. (Chiefly in wild form).—Chinese hickory.
81. *Corylus heterophylla* Fisch., *C. ferox* Wall., *C. colurna* L. (The last two species are also found in their wild form in Nepal, Sukhum, and Kamaon), and other species.—Hazelnut. (Chiefly wild).
82. *Castanea crenata* Sieb. and Zucc., *C. mollissima* Bl.—An East Asiatic chestnut. (The first species is found in Japan and Korea, the second in China).
83. *Torreya grandis* Fort.
84. *Pinus koraiensis* Sieb. and Zucc.—Korean pine. (Korea, Japan, Manchuria).

Group of subtropical and tropical zones

85. *Citrus junos* (Sieb.) Tanaka.
86. *Citrus ichangensis* Swingle.
87. *Citrus sinensis* Osb—Orange. (A very important secondary center). This species has a great number of varieties.
88. *Citrus nobilis* Lour. (Probably a secondary center); *C. ponki* Tan. (Endemic to China); *C. tarbiferox* Tan. (Endemic to China); *C. erythrosa* Tan. (Endemic); *C. kinokuni* Tan. (Endemic to China and Japan); *C. amblycarpa* (Hassk.).—Tangerines.
89. *Fortunella margarita* Swingle—Kumquat. (Typical endemic Chinese species, as are the other species of kumquats).
90. *Fortunella japonica* Swingle; *F. crassifolia* Swingle.
91. *Poncirus trifoliata* Kaf.—Trifoliate orange.
92. *Diospyros kaki* L. and *D. sinensis* Bl.—Persimmon.
93. *Diospyros lotus* L.—Date plum (Wild and grafted).
94. *Eriobotrya japonica* Lindl.—Loquat.
95. *Clausena lansium* Skeels.—Wampi.
96. *Myrica rubra* S. and Z.
97. *Litchi chinensis* Sonn.—Litchi.
98. *Nephelium longanum* Cambess.—Litchi.
99. *Rhodomyrtus tomentosa* Wight—Hill gooseberry.

SUGAR PLANTS:—

100. *Saccharum sinense* Roxb—An endemic group of sugar cane varieties.

OIL, ETHEREAL OIL, RESIN, AND TANNIN PLANTS:—

101. *Perilla ocymoides* L.
102. *Raphanus sativus* var. *oleifera* Metzg—Oil-bearing radish.
103. *Aleurites fordii* Hemsl., *A. montana* Wilson, *A. cordata* R. Br.—Wood-oil tree. The species *A. cordata* is distributed chiefly throughout Japan.
104. *Camellia sasanqua* Thunb., *C. japonica* L.
105. *Melia azedarach* L.—Chinaberry.
106. *Sesamum indicum* L.—Sesame. Special endemic group of dwarf varieties. (Secondary center).

SPICE PLANTS:—

107. *Zanthoxylum bungei* Planch.
108. *Zanthoxylum piperitum* DC., *Z. planispinum* Sieb. and Zucc.
109. *Fagara schinifolia* (Sieb. and Zucc.) Engl. (var. *macrocarpa* Loes).
110. *Cinnamomum cassia* L.—Chinese cinnamon.
111. *Illicium anisatum* (L.) Gaertn. (*I. verum* Hook. f.) (Japan included).
112. *Camellia sinensis* (L.) O. Ktze. (*Thea sinensis* L.).—Tea bush.

TECHNICAL AND MEDICINAL PLANTS:—

113. *Sapindus mukorosi* Gaertn.—(Used in soap).
114. *Eucomia ulmoides* Oliv.—(Rubber tree found chiefly wild).
115. *Sapium sebiferum* Roxb. (*Stillingia sebifera* Michx.)—Chinese oil (lard) tree.
116. *Rhus vernicifera* Stockes; and other species.—Lacquer tree.
117. *Rhus succedanea* L.—Wax tree.
118. *Broussonetia papyrifera* Vent., *B. kasinoki* Sieb. and other species.—(Used for paper).
119. *Morus alba* L.—Mulberry tree; also *M. bombycis* Koidzumi, *M. multicaulis* Perr. (*M. alba* L.)
120. *Cinnamomum camphora* Nees and Eberm.—Camphor tree.
121. *Papaver somniferum* L.—Opium poppy. (An unusual diversity of varieties).
122. *Panax ginseng* C. A. May.—Ginseng.
123. *Aconitum wilsonii* Hort.—Aconite.
124. *Smilax china* L.

FIBER PLANTS:—

125. *Boehmeria nivea* Hook. and Arn., *B. tenacissima* Gaud.—Ramie.
126. *Cannabis sativa* L.—A hemp with large fruits.
127. *Abutilon avicennae* Gaertn.
128. *Trachycarpus excelsus* Makino—Fiber palm.
129. *Themeda triandra* Forsk. var. *japonica* Makino.
130. *Metroxylon sagu* Rottb.—(Used for roof covering and as food in the Sunda Islands).

PLANTS USED FOR MANUFACTURING DYES:—

131. *Polygonum tinctorium* Lour.
132. *Strobilanthes flaccidifolius* Nees—(For blue dye).
133. *Rubia cordifolia* L.—Madder.
134. *Lithospermum erythrorrhizon* S. and Z.

PLANTS OF MISCELLANEOUS USES:—

135. *Astragalus sinicus* L.—Chinese Astragalus, used as green manure.
136. *Cycas revoluta* Thunb.—Sago palm (Japan).

The most important endemic plants of the temperate zone are three species of millet, buckwheat, soy bean, and a number of legumes. Here we find an unusually large number of plants with tubers and thickened taproots, and aquatic plants which are peculiar to China. *China occupies first place in the wealth of fruit species of Pyrus, Malus, Prunus. Many citrus fruits have their origin in China.* The cultivated plants of China are peculiar and differ in their makeup from those of other primary centers of agriculture of the world. Both the vegetable and the animal foods of the Chinese are unusual. The customary diet of the Chinese includes shoots of various bamboos; numerous cultivated aquatic plants, including the grass, *Zizania latifolia,* which is grown for the smutted leaf sheaths; edible burdock; strange chinese cabbages; giant radishes weighing up to 36 pounds; a host of dishes prepared from the soy bean which takes the place of meat; and toffu-cheese. *In wealth of its endemic species and in the extent of the genus and species potential of its cultivated plants, China is conspicuous among other centers of origin of plant forms.* Moreover, the species are usually represented by enormous numbers of botanical varieties and hereditary forms. The varieties of the soy bean, adzuki bean, persimmon, and citrus fruits include thousands of easily distinguished hereditary forms.

It is noteworthy that this diversity of plants of the temperate and subtropical zones is in evidence chiefly around the eastern and central sections of China.[8]

II. *The Indian Center of Origin of Cultivated Plants* (Exclusive of Northwest India, Punjab, and Northwest frontier, but including Assam and Burma).—*Second in importance and in geographic order is the Indian or, more exactly, the Hindustan center of origin of cultivated plants, which includes Burma and Assam and excludes Northwest India—Punjab, and the northwestern frontier provinces.*

CEREALS:— ✓

1. *Oryza sativa* L.—Rice. (Cultivated in enormous variety, also wild).
2. *Andropogon sorghum* Brot.—Sorghum. An unusually large geographic group. (Secondary origin).
3. *Eleusine coracana* Gaertn.—African millet. (One of the centers of origin); *E. indica* (L.) Gaertn.—Wiregrass. A wild weed form. (Its young plants are used as a vegetable).
4. *Paspalum scrobiculatum* L.—Cultivated and wild.

LEGUMES:— ✓

5. *Cicer arietinum* L.—Chick pea.
6. *Cajanus indicus* Spreng.—Pigeon pea.

[8] If we take into account the enormous number of wild plants, besides the cultivated ones, used for food in China, we may better understand how hundreds of millions of people manage to exist on its soil.

7. *Phaseolus aconitifolius* Jack. (*Ph. trilobus* Willd.).—Mat bean. Wild and cultivated.
8. *Phaseolus mungo* L.—Urd or black gram.
9. *Phaseolus aureus* (Roxb.) Piper.—Mung bean.
10. *Phaseolus calcaratus* Roxb. (Cultivated and wild).—Rice bean.
11. *Dolichos biflorus* L. (Cultivated and wild).
12. *Dolichos lablab* L.—Hyacinth bean.
13. *Vigna sinensis* Endl.—Cowpea.
14. *Trigonella foenum graecum* L.—Fenugreek. (Independent center of origin).
15. *Canavalia gladiata* DC.—Sword bean. (Wild and cultivated).
16. *Pachyrrhizus angulatus* Rid.—Yam bean. (Possibly also found in Indo-China).
17. *Psophocarpus tetragonolobus* DC.—Asparagus bean.
18. *Cyamopsis psoralioides* DC.—Guar.

OTHER GRAINS :—

19. *Amarantus frumentaceus* Roxb.; *A. speciosus* Sims ; *A. anardana* Wallich.—Amaranth.

VEGETABLES :—

20. *Amarantus blitum* var. *oleraceus* Watt.—(Wild and cultivated).
21. *Amarantus gangeticus* L.; *A. tricolor* L.
22. *Solanum melongena* L.—Eggplant.
23. *Carum roxburghianum* Benth. and Hook.; *C. copticum* Roxb.—(One of the centers of origin).
24. *Momordica charantia* L.—Balsam pear.
25. *Cucumis sativus* L.—Cucumber. Here is also found its closely related wild species, *Cucumis hardwickii* Royle.
26. *Raphanus caudatus* L.—Radish. (The pods are used as food).
27. *Lagenaria vulgaris* Ser.—White flowered gourd.
28. *Luffa acutangula* Roxb.—Dishcloth gourd.
29. *Trichosanthes anguina* L. and other species.—Serpent gourd, etc.
30. *Basella rubra* L.—Malabar nightshade.
31. *Pluchea indica* (L.) Less.—Marsh fleabane. (Wild and cultivated).
32. *Anethum sowa* Roxb. (*Peucedanum graveolens* Wats).—Indian parsley. (Also medicinal).
33. *Lactuca indica* L.—Indian lettuce.

PLANTS WITH EDIBLE ROOTS AND ROOT TUBERS :—

34. *Colocasia antiquorum* Schott.—Elephant's ear. (Wild and cultivated; one of the centers of origin).
35. *Alocasia macrorrhiza* Schott. (*Arum macrorrhizum* L.). Especially numerous on the island of Ceylon and other islands; wild and cultivated.
36. *Dioscorea alata* L., *D. aculeata* L.—Yam. (Wild and cultivated; possibly also in the Malay Peninsula).
37. *Curcuma zedoaria* Rosc., *C. longa* Roxb., and other species. (Used for starch and in medicine).
38. *Amorphophallus campanulatus* Blume. (Wild and cultivated).
39. *Raphanus indicus* Sinsk.—Indian radish.

CULTIVATED FRUITS :—

40. *Mangifera indica* L.—Mango. (Wild and cultivated).
41. *Citrus sinensis* Osb.—Orange. (Wild and cultivated).
42. *Citrus poonensis* Tan.
43. *Citrus nobilis* Lour.—Tangerine.
44. *Citrus limonia* Osb.—Canton lemon. (Cultivated and wild) (?). *Citrus limon* Burm. f.—Lemon.
45. *Citrus medica* L.—Citron. (Cultivated and wild).
46. *Citrus aurantium* L.—Sour orange. Wild and cultivated.
47. *Citrus aurantiifolia* (L.) Swingle.—Sour lime. (Chiefly on the islands).
48. *Terminalia bellerica* Roxb. (Cultivated and wild).
49. *Phoenix silvestris* Roxb.—Wild date. (Cultivated and wild).
50. *Garcinia indica* Choisy. (Cultivated and wild).
51. *Mimusops elengi* L.—Spanish cherry. (Cultivated and wild).
52. *Feronia elephantum* Correa. (Cultivated and wild).
53. *Eugenia jambolana* Lam. (*E. jambos* L.)—Jambos or jambolan plum. Cultivated and wild; one of the centers of origin.

54. *Artocarpus integra* (Thunb.) Merr. (*A. integrifolia* L.)—Jack fruit. Cultivated and wild. (One of the centers of origin).
55. *Aegle marmelos* Correa—Ball fruit. (Also used for resin production, medicinally, and as a dye).
56. *Averrhoa bilimbi* L.—Bilimbi. (Cultivated and wild).
57. *Averrhoa carambola* L.—Carambola. (Ceylon and also the Islands of Molucca).
58. *Carissa carandas* L.—Karanda. (Usually wild, also in cultivation).
59. *Phyllanthus emblica* L., and other species.—Myrobalan, etc. (Cultivated and wild).
60. *Murraya exotica* L., *M. koenigii* Sér. (Cultivated and wild).
61. *Morinda citrifolia* L.—Indian mulberry. (Cultivated and wild).
62. *Mimusops hexandra* Roxb. (Cultivated and wild).
63. *Tamarindus indica* L. (?)—Tamarind. (It is not impossible that this has been introduced from Africa).

SUGAR PLANTS :—

64. *Saccharum officinarum* L.—Sugar cane.
65. *Arenga saccharifera* Labill.—Sugar palm. (Also common on the Malay Archipelago).

OIL PLANTS :—

66. *Cocos nucifera* L.—Cocoanut palm. (One of the centers of origin, growing chiefly in Southern India).
67. *Sesamum indicum* L.—Sesame. (Basic center of origin of cultivated sesame).
68. *Carthamus tinctorius* L.—Safflower. (One of the centers of origin).
69. *Brassica juncea* Czern.—Leaf mustard. (Possibly a secondary center of origin).
70. *Brassica glauca* Wittm.—(Possibly a secondary center of origin).
71. *Brassica nigra* Czern.—Black mustard. A separate geographic group. (Secondary).

FIBER PLANTS :—

72. *Gossypium arboreum* L.—Tree cotton.
73. *Gossypium nanking* Meyen and *G. obtusifolium* Roxb.—Oriental cotton.
74. *Corchorus capsularis* L., *C. olitorius* L. and others.—Jute.
75. *Crotalaria juncea* L.—Crotalaria.
76. *Sesbania aculeata* Pers.—Sesbania.
77. *Hibiscus cannabinus* L.—Kenaf.
78. *Hibiscus sabdariffa* L.—Roselle. (Flower buds are used as food).
79. *Bombax malabaricum* DC. (Cultivated and wild).
80. *Sida rhombifolia* L. (Cultivated and wild).
81. *Abroma augusta* L. f.
82. *Sansevieria zeylanica* Willd.—Bowstring hemp.

SPICE PLANTS AND STIMULANTS :—

83. *Cannabis indica* L.—Hemp. (Used for hasheesh).
84. *Piper nigrum* L.—Black pepper. (Wild and cultivated).
85. *Piper betle* L., *P. longum* L., and other species.—Betle nut.
86. *Elettaria cardamomum* Maton and White, *E. major* Smith—Cardamon.
87. *Areca catechu* L.—Areca palm. (Probably a secondary center of origin). Chiefly in Ceylon.
88. *Alpinia galanga* Willd. and other species.
89. *Kaempferia galanga* L.
90. *Curcuma mangga* Val. et v. Zijp., *C. purpurascens* Bl., *C. xanthorrhiza* Roxb.
91. *Cuminum cyminum* L.—Cumin.

ETHEREAL OIL PLANTS, RESIN AND TANNIN PLANTS :—

92. *Acacia arabica* Willd.—Gum arabic.
93. *Acacia catechu* Willd.—(Also used in dye manufacture).
94. *Acacia farnesiana* Willd.
95. *Cymbopogon martini* Stapf. *C. nardus* Rendle.—Citronella grass.
96. *Pogostemon heyneanus* Benth. (*P. patchouli* Pellet.).
97. *Santalum album* L.—Sandalwood.
98. *Jasminum grandiflorum* L.—Poet's jessamine.

PLANTS USED IN MANUFACTURE OF DYES :—

99. *Indigofera tinctoria* L.—Indigo. (Possibly introduced from China).
100. *Morinda citrifolia* L.—Indian mulberry.
101. *Rubia tinctorum* L.—Madder.
102. *Lawsonia alba* Lam.—Henna. (Wild and cultivated; it was cultivated as early as the time of ancient Egypt).

103. *Oldenlandia umbellata* L.
104. *Caesalpinia sappan* L.
105. *Terminalia catappa* L.—Indian almond. (Cultivated and wild).
106. *Terminalia chebula* Retz. and other species.—(Cultivated and wild).

MEDICINAL PLANTS:—

107. *Cassia angustifolia* Vahl.—Senna. (Wild and cultivated).
108. *Cinnamomum zeylanicum* Breyn.—Cinnamon tree. (Wild and in cultivation—also a spice).
109. *Croton tiglium* L.—Croton.
110. *Strychnos nux vomica* L.—Strychnin nut.
111. *Taraktogenos kurzii* King.—Chaulmoogra oil tree.
112. *Hydnocarpus anthelmintica* Pierr.
113. *Oroxylum indicum* (L.) Vent.

MISCELLANEOUS:—

114. *Bambusa tulda* Roxb.—Bamboo. (Cultivated and wild).
115. *Cedrela toona* Roxb. (In cultivation and wild).—Used for various purposes.
116. *Borassus flabellifer* L.—Palmyra palm. (Cultivated and wild).
117. *Ficus elastica* Roxb.—Rubber plant.

India is undoubtedly the birthplace of rice, sugar cane, a large number of legumes, and many tropical fruit plants, including the mango and numerous citrus plants (e.g., the orange, lemon, some species of tangerine). Assam, in particular, is most remarkable for its citrus plants.

Even though tropical India may stand second to China in the number of species, its *rice,* which was introduced to China, where it has been the staple food plant for the past thousand years, makes tropical India even more important in world agriculture. That India is the native home of rice is borne out by the presence there of a number of wild rice species, as well as common rice, growing wild, as a weed, and possessing a character common to wild grasses, namely, shedding of the grain at maturity, which insures self-sowing. Here are also found intermediate forms connecting wild and cultivated rice. The varietal diversity of the cultivated rice of India is the richest in the world, the coarse-grained primitive varieties being especially typical. India differs from China and other secondary regions of cultivation in Asia by the prevalence of dominant genes in its rice varieties.

In India, as in China, a large number of wild plants are used for various purposes including food.[4]

IIa. *The Indo-Malayan Center of Origin of Cultivated Plants* (Including Indo-China and the Malay Archipelago.)—In addition to the Indian center we distinguish the Indo-Malayan center which includes the entire Malay Archipelago, the large islands such as Java, Borneo, and Sumatra, the Philippines, and Indo-China.

CEREALS:—

1. *Coix lacryma* L.—Job's-tears. (Mostly indigenous to islands).

LEGUMES:—

2. *Mucuna utilis* Wall. and Wight. (Sunda Islands).

BAMBOOS:—

3. *Dendrocalamus asper* (Schult.) Backer.—Giant bamboo. (Sunda Islands).
4. *Gigantochloa apus* (Roem. and Schult.) Kurz., *G. ater* Kurz., *G. verticillata* (Willd.) Munro (most commonly cultivated on the Sunda Islands).

THICKENED TAPROOTS AND ROOT TUBERS:—

5. *Dioscorea alata* L. (On islands), *D. hispida* Dennst.—Yams.
6. *Dioscorea pentaphylla* L. (Wild and cultivated in Java).—Yams.
7. *Dioscorea bulbifera* L.—Air potato.

[4] See WATT, *Dictionary of Economic Plants;* DRURY, *The Useful Plants of India*, London, 2 ed. 1873; and others.

8. *Coleus tuberosus* (Bl.) Benth.—Leaves, stems and tubers are used for food. (Sunda Islands).
9. *Phytolacca esculenta* Van Houtte.—Pokeweed. (Possibly also in India).
10. *Tacca pinnatifida* Forst. (Especially common on the islands of Fiji, Samoa, and the New Hebrides).
11. *Zingiber officinale* Rosc., *Z. mioga* Rosc., *Z. zerumbet* Rosc.—Ginger; also used as a spice plant. (The second species also refers to Japan).
12. *Benincasa hispida* Cogn.—Wax gourd.
13. *Sauropus androgynus* (L.) Merr.—(On Sunda Islands).
14. *Abelmoschus manihot* (L.) Medic.

CULTIVATED FRUITS:—

15. *Citrus microcarpa* Bge., *C. mitis* Bl.—Calamondin. The first species is most common in Java.
16. *Citrus grandis* Osb. (*C. maxima* Merr.)—Pummelo. (Found chiefly on islands).?
17. *Citrus hystrix* (DC). Ang. (On islands).
18. *Nephelium mutabile* Bl. (On islands).—Wild and in cultivation.
19. *Canarium pimela* Koenig, *C. album* Roensch.
20. *Areca catechu* L.—Areca palm. (Sunda Islands, Malacca). Wild and cultivated. (Basic center).
21. *Erioglossum rubiginosum* (Roxb.) Brandes, *E. edule* Bl.
22. *Antidesma delicatulum* Hutch., *A. hainanensis* Merr., *A. bunias* (L.) Spreng.
23. *Musa cavendishii* Lamb., *Musa paradisiaca* L., *M. sapientum* L.—Banana. (The two last species are mostly indigenous to the islands).
24. *Garcinia mangostana* L.—Mangosteen, *G. dulcis* (Roxb.) Kurz. Wild and cultivated.
25. *Artocarpus communis* Forst., *A. champeden* (Lour.) Spreng.—Breadfruit. (Malay Archipelago).
26. *Artocarpus integra* (Thunb.) Merr.—Jackfruit.
27. *Durio zibethinus* Murr.—Durian. (Malay Archipelago).
28. *Lansium domesticum* Corr.—(Malay Archipelago).
29. *Bouea macrophylla* Griff.—(Malay Archipelago).
30. *Mangifera caesia* Jack., *M. foetida* Lour., *M. odorata* Griff.—(Malay Archipelago).
31. *Baccaurea racemosa* (Bl.) Muell. (Java and the Philippines).
32. *Flacourtia rukam* Zoll. and Mor. (Wild and cultivated on Java).
33. *Pangium edule* Reinw. and Bl. (Wild and cultivated on the Sunda Islands).
34. *Pithecolobium lobatum* Benth. (Sunda Islands).
35. *Cynometra cauliflora* L. (On islands).
36. *Sandoricum koetjape* (Burm.) Merr. f. Wild and cultivated (Java).
37. *Eugenia aquea* Burm. f., *E. cuminii* (L.) Merr.—Jambolan plum, *E. jambos* L.—Rose apple, *E. javanica* Lam., *E. malaccensis* L.—Malay apple. (On the Malacca, Java and other islands).
38. *Nephelium lappaceum* (L.) Wight.
39. *Salacca edulis* Reinw.—Salacca palm.
40. *Rubus rosaefolius* Smith—(Introduced into cultivation in Java; also found wild on the Philippine Islands; extends as far as southern Japan).

OIL PLANTS:—

41. *Aleurites moluccana* (L.) Willd.—Candlenut. (On Sunda Islands).
42. *Cananga odorata* (Lam.) Hook. and Thoms. f.—Ylang-ylang. (Probably from Malay).
43. *Vetiveria zizanioides* Stapf.—Vetiver. (Probably from Malay).
44. *Cocos nucifera* L.—Cocoanut palm. (Probably basic center of origin).

SUGAR PLANTS:—

45. *Saccharum officinarum* L.—Sugar cane. One of the centers of origin.
46. *Arenga saccharifera* Labill.—Sugar palm. One of the centers of origin. (Possibly the main one).

SPICE PLANTS:—

47. *Elettaria cardamomum* Maton and White.—Cardamon. Wild and cultivated on the Sunda Islands. Also *Amomum krevanh* Pierre. (Wild and cultivated).
48. *Kaempferia galanga* L., *K. pandurata* Roxb., *K. rotundata* L. (Growing on Sunda Islands).
49. *Caryophyllus aromaticus* L. (*Eugenia caryophyllata* Thunb.).—Clove tree. (The Moluccas and other islands).

50. *Myristica fragrans* Houtt.—Nutmeg. Wild and cultivated. (On the Moluccas and other islands).
51. *Piper nigrum* L.—Black pepper.

FIBER PLANTS:—

52. *Musa textilis* Née—Manila hemp or abaca. (Philippine Islands).
53. *Metroxylon sagu* Rottb.—(Used for roofing and also as food on the Sunda Islands).

PLANTS USED IN THE MANUFACTURE OF DYES:—

54. *Curcuma longa* L.—Curcuma. (One of the centers of origin).

RUBBER PLANTS:—

55. *Palaquium gutta* Bursck—Gutta-percha tree.

Unfortunately, the region of southeastern Asia, with its wealth of tropical wild and cultivated flora, has as yet been insufficiently explored, and it may be necessary later to make numerous additions to and perhaps changes in the foregoing list of the species.

This center, supplementing the center of India, is rich in cultivated fruits of worldwide economic importance, such as the banana and certain citrus fruits. The wild flora includes a large number of useful plants which have been especially well studied by Dutch scientists in Java.[5]

III. *The Central Asiatic Center of Origin of Cultivated Plants.*—The third center of formation of cultivated plants embraces a comparatively smaller territory. We refer to it as the Central Asiatic center. It includes northwest India (Punjab, the northwestern frontier provinces, Kashmir), all of Afghanistan, our Soviet Republics of Tadjikistan and Uzbekistan, and western Tian-Shan.

CULTIVATED GRAIN CROPS:—

1. *Triticum vulgare* Vill.—Common wheat.
2. *Triticum compactum* Host—Club wheat.
3. *Triticum sphaerococcum* Perc.—Shot wheat.
4. *Secale cereale* L.—Rye. (Secondary center).
5. *Pisum sativum* L.—Pea.
6. *Lens esculenta* Moench.—Lentil.
7. *Vicia faba* L.—Beans.
8. *Lathyrus sativus* L.—Grass pea.
9. *Cicer arietinum* L.—Chick pea.
10. *Phaseolus aureus* Roxb.—Mung bean.
11. *Phaseolus mungo* L.—Urd or black gram. (*Ph. radiatus* Roxb.)—Secondary center.
12. *Brassica campestris* subsp. *oleifera* Metzg.—Rape. (Secondary center).
13. *Brassica juncea* Czern.—Mustard.
14. *Eruca sativa* Lam.—Rocket-salad. (A weed; one of the centers of origin).
15. *Lepidium sativum* L.—Garden cress. (Secondary center).
16. *Linum usitatissimum* L.—Flax. (One of the centers of origin).
17. *Sesamum indicum* L.—Sesame. (One of the centers of its origin).
18. *Coriandrum sativum* L.—Coriander. (One of the centers of origin).
19. *Carum copticum* Benth. and Hook. (*Ammi copticum* L.).
20. *Carthamus tinctorius* L.—Safflower. (One of the centers of origin).
21. *Cannabis indica* Lam.—Hemp.

FIBER PLANTS:—

22. *Gossypium herbaceum* L.—Cotton.

VEGETABLES:—

23. *Cucumis melo* L.—Cantaloupe. (Secondary center).
24. *Lagenaria vulgaris* Sér.—White flowered gourd. (Secondary center).
25. *Daucus carota* L.—Carrot. (Basic center of Asiatic varieties).
26. *Brassica campestris* L. subv. *rapifera* Metzg.—Turnip. (Basic center of Asiatic turnips).
27. *Raphanus sativus* L.—Radish. (One of the centers of origin).

[5] See OCHSE, J. J. *Vegetables of the Dutch East Indies.* Buitenzorg, Java; *Fruits of the Dutch East Indies,* by the same author, 1933; and HEYNE, K. *De nuttige planten van Nederlandsch Indië,* 2nd ed. (3 volumes), 1927. Buitenzorg.

28. *Allium cepa* L. (*sensu lato*).—Onion. (Cultivated). Here are also found growing wild the related species: *A. pskemense* Fedtsch., *A. vavilovii* Vved.
29. *Allium sativum* L.—Garlic. (Cultivated and wild); *A. longicuspis* E. Regel.
30. *Spinacia oleracea* L.—Spinach. Also here the related wild species, *S. tetrandra* Stev.
31. *Portulaca oleracea* L.—Kitchen garden purslane. (One of the centers).

SPICE PLANTS:—

32. *Ocimum basilicum* L.—Basil.

CULTIVATED FRUITS:—

33. *Pistacia vera* L.—Pistachio. (One of the centers).
34. *Prunus armeniaca* L.—Apricot. (One of the centers).
35. *Pyrus communis* L.—Pear. Also growing wild, *P. heterophylla* Reg. and Schmalh., *P. korshinskyi* Litw., *P. vavilovii* M. Pop., *P. bucharica* Litw.
36. *Amygdalus communis* L.—Almond. (Wild and cultivated). (One of centers of origin, very diversified in the species it contains). Here are also found *A. bucharica* Korsh., *A. spinosissima* Bge, both growing wild.
37. *Eleagnus angustifolia* L.—Russian olive. (One of the centers).
38. *Zizyphus sativa* Gaertn.—Jujube. Wild and cultivated. (One of the centers).
39. *Vitis vinifera* L.—Grape. (Wild and in cultivation).[6]
40. *Juglans regia* L.—English walnut. (Cultivated and wild). One of the centers.
41. *Corylus colurna* L.—Turkish hazelnut. (Chiefly wild, in Afghanistan).
42. *Malus pumila* Mill.—Apple. Grows wild in great variety, especially in Western Tian-Shan. Also in cultivation. (One of the centers).

The number of species in this center is much smaller than in the two preceding; nevertheless, it is of great importance to us for it is the *native home of common wheat.* Here is the location of a tremendous potential source of varieties of common wheat—the principal bread grain of the earth. *This is the birthplace of club wheat, of shot wheat, and of all the chief legumes, such as peas, lentils, beans, grass peas, and chick peas; all of which are exceptionally rich in the number of genes.* Here many oil plants have had their origin; and here cotton, was probably first cultivated on a broad scale.

The uniform ecological conditions and the uniform wild and cultivated floras of Punjab, Kashmir, and the eastern part of Soviet Central Asia necessitate regarding these regions as one center. In spite of the barrier presented by the Himalayas and Hindu-Kush, it seems necessary to combine a large part of Middle Asia and Northwest India into one center.

IV. *The Near-Eastern Center of Origin of Cultivated Plants.— The fourth center occupies the Near East, including the interior of Asia Minor, the whole of Transcaucasia, Iran, and the highlands of Turkmenistan.*

CULTIVATED GRAIN CROPS:—

1. *Triticum monococcum* L.—Einkorn wheat. (14 chromosomes). Here are also found widely-distributed the wild single-seeded *Triticum thaoudar* Reut. and *Tr. aegilopoides* Perc.
2. *Triticum durum* subsp. *expansum* Vav.—Durum wheat. (28 chromosomes).
3. *Triticum turgidum* L. *mediterraneum* Flaksb.—Poulard wheat. (28 chromosomes).
4. *Triticum vulgare* Vill.—An endemic awnless group of common wheats. (42 chrom.). One of the centers of origin.
5. *Triticum orientale* Perc.
6. *Triticum persicum* Vav.—Persian wheat. (28 chromosomes). Armenia and Georgia.
7. *Triticum timopheevi* Zhuk.—(28 chrom.).
8. *Triticum macha* Dekapr. (42 chrom.).
9. *Triticum vavilovianum* Jakub. (*Tr. vulgare compositum* Tum.). — An unusual branched wheat found by Prof. M. G. Tumanyan near Lake Van in Turkish Armenia (42 chrom.). Here are also found large quantities of wild wheat, *Tr. dicoccoides* Körn. (Armenia, Nakhichevan) and a large number of endemic species of *Aegilops.*

[6] Here the wild grape, *Vitis vinifera spontanea* M. Pop., is of table quality, *i.e.,* it closely resembles the cultivated grapes. These grapes are at present found only within the boundaries of Tadjikistan. The *Vitis silvestris* C. Gmel., which has given rise to the wine-producing grape varieties, is not found here (M. Popov).

10. Endemic group of cultivated two-rowed barleys—(*Hordeum distichum* vv. *medicum, nigricans, nutans,* and others).
11. *Secale cereale* L.—Rye; here there are also the wild species, *S. montanum* Guss., *S. ancestrale* Zhuk., *S. vavilovii* Grossh., *S. fragile* L., *S. villosum* L. (*Haynaldia villosa* Schur.).
12. *Avena byzantina* C. Koch—Mediterranean oats.
13. *Avena sativa* L.—Common oats. A great number of endemic varieties growing as weeds in cultivated fields, especially in Transcaucasia.
14. *Cicer arietinum* subsp. *pisiforme* G. Pop.—Chick pea. (Secondary center).
15. *Lens esculenta* Moench—Lentil. A large endemic group of varieties. Here there are found also the wild forms: *Lens lenticula* (Schreb) Alef., *L. nigricans* (M. B.) Godr., *L. kotschyana* (Boiss.) Alef., *L. orientalis* (Boiss.) Hand.—Mazz.
16. *Vicia ervilia* Willd.—French lentil—a separate endemic group.
17. *Pisum sativum* L.—Pea. A large endemic group. (Secondary center). Here are also found wild species of peas: *P. elatius* M. B., *P. humile* Boiss., *P. fulvum* Sibth. et Sm.
18. *Lupinus pilosus* L., *L. angustifolius* L.—Blue lupine; *L. albus* L—White lupine;—wild and in cultivation in Asia Minor.

FORAGE PLANTS:—

19. *Medicago sativa* L—Blue alfalfa.
20. *Trifolium resupinatum* L.—Persian clover
21. *Trigonella foenum graecum* L.—Fenugreek. Cultivated and wild (Secondary center).
22. *Onobrychis altissima* Grossh., *O transcaucasica* Grossh.—(Two Transcaucasian species, wild and in cultivation).
23. *Lathyrus cicera* L. (One of the centers).
24. *Vicia sativa* L.—Crop vetch; a large endemic group of varieties in Asia Minor. (Basic center of formation for this species).
25. *Vicia villosa* Roth var. *perennis* Tum—Hairy vetch, wild-growing; is being introduced into cultivation.
26. *Vicia pannonica* Jack.—Hungarian vetch. Cultivated and growing as a weed.

OIL PLANTS:—

27. *Sesamum indicum* L. subsp *bicarpellatum* Hillt.—Sesame. (A separate geographic group).
28. *Linum usitatissimum* L.—Flax—Many endemic varieties. The group *prostratum* Vav. is endemic in Asia.
29. *Brassica campestris* L. subsp. *oleifera* Metzg.—Rape. (Secondary center).
30. *Brassica nigra* L. var *pseudocampestris* Sinsk. and var. *orientalis* Sinsk—Black mustard. (One of the centers).
31. *Brassica juncea* Czern. var. *sareptana* Sinsk—Leaf mustard. Secondary center.
32. *Camelina sativa* L.—False flax. Cultivated and growing as weed.
33. *Eruca sativa* L. var. *orientalis* Sinsk.—Rocket salad.
34. *Cephalaria syriaca* Schrad.
35. *Ricinus persicus* G. Popova—A caster-oil plant with small seeds. (Secondary center).

ETHEREAL OIL, ALKALOID, AND TANNIN PLANTS:—

36. *Pimpinella anisum* L—Anise.
37. *Pimpinella anisetum* Boiss.—Anisette.
38. *Coriandrum sativum* L.—Coriander. (One of the centers).
39. *Lallemantia iberica* L.—A field weed and cultivated plant.
40. *Papaver somniferum* L.—Poppy. A large group of endemic forms with high morphine content.
41. *Rosa centifolia* L.—Rose.
42. *Rhus coriaria* L.—Sumac. Mostly wild.

MELON PLANTS:—

43. *Cucumis melo* L.—Cantaloupe. Also wild forms: *Cucumis agrestis* Pang. and *C. microcarpus* Pang. All basic world varieties of the cantaloupe are concentrated in Near Asia.
44. *Cucumis flexuosus* L.—Serpent melon.
45. *Cucumis sativus* L. subsp. *antasiaticus* Gabaiev.—Anatolian cucumber. A separate geographic race.
46. *Cucurbita pepo* L.—Pumpkin. The greatest diversity of varieties is concentrated in Asia Minor.[7]

[7] The question of the origin of *Cucurbita pepo* requires further investigations.

VEGETABLES :—

47. *Lepidium sativum* L.—Garden cress. (Secondary origin).
48. *Brassica campestris* var. *rapifera* Metzg.—Turnip. (Secondary center).
49. *Beta vulgaris* L.—Garden beet. There exists a separate geographic group of forms in Near Asia. (Secondary center).
50. *Daucus carota* L.—Carrot. There is an unusually great variety of cultivated forms in Anatolia.
51. *Brassica oleracea* L.—Cabbage. In Anatolia there are many endemic forms.
52. *Eruca sativa* L.—Rocket salad. (A weed form; the leaves are utilized).
53. *Allium cepa* L.—Onion. (Secondary center).
54. *Allium porrum* L.—Leek. (There are present some closely related wild species such as *A. ampeloprasum* L. and others).
55. *Petroselinum hortense* Hoffm.—Parsley. (Secondary center).
56. *Lactuca sativa* L.—Lettuce, wild and cultivated.
57. *Portulaca oleracea* L.—Purslane. Present as a weed and in cultivated form.

CULTIVATED FRUITS :—

58. *Ficus carica* L.—Fig.
59. *Punica granatum* L.—Pomegranate.
60. *Malus pumila* Mill.—Apple. (One of the centers).
61. *Pyrus communis* L. and other species, such as *P. salicifolia* Pall., *P. eleagrifolia* Pall., *P. syriaca* Boiss., *P. nivalis* Jacq.—Pear.
62. *Cydonia oblonga* Mill.—Quince.
63. *Prunus divaricata* Led.—Cherry.
64. *Prunus cerasus* L.—Cherry. (The center of origin may possibly be in Asia Minor; this, however, is subject to proof).[8]
65. *Cerasus avium* (L.) Mönch—Black cherry.
66. *Amygdalus communis* L., *A. fenzliana* Lipsky, *A. bucharica* Korsh., *A. scoparia* Spach., *A. spinosissima* Bge., and other species.—Almond, etc. Mostly growing wild.
67. *Laurocerasus officinalis* Roem.—Cherry laurel.
68. *Mespilus germanica* L.—Medlar.
69. *Juglans regia* L.—English walnut. (One of the centers).
70. *Corylus avellana* L.—European hazelnut. (Cultivated and growing wild). Also wild species: *C. maxima* Mill.—Filbert; *C. pontica* Koch, *C. colurna* L.—Turkish hazelnut, and *C. colchica* Alb.
71. *Castanea sativa* Mill. (*C. vesca* Gaertn.)—Chestnut. One of the centers.
72. *Zizyphus sativa* Gaertn.—Jujube. (Secondary center).
73. *Vitis vinifera* L.—Grape. (In enormous diversity of forms). Cultivated and wild.
74. *Berberis vulgaris* L.—Barberry.
75. *Prunus armeniaca* L.—Apricot. (One of centers of origin, probably a secondary one).
76. *Prunus padus* L.—European bird cherry. One of the centers.
77. *Pistacia vera* L.—Pistachio. (One of centers).
78. *Eleagnus angustifolia* L.—Russian olive.
79. *Diospyros lotus* L.—Date-plum.
80. *Cornus mas* L.—Cornelian cherry.
81. *Crataegus azarolus* L.—Hawthorn.

SPICES AND PLANTS USED FOR DYE AND MANUFACTURE :—

82. *Crocus sativus* L.—Saffron crocus. It is possible that this plant also belongs to the Mediterranean center. (Greece, Italy).
83. *Rubia tinctorum* L.—Madder. (Wild and cultivated).

Recent research has shown that this center is most notable for its wealth of varieties of cultivated wheats. *Nine botanical species of wheat are endemic in the Near East.*

Within the limits of the SSSR the greatest diversity of wheats is found in Armenia, surpassing the number of varieties and species in all other parts of the Union. M. G. TUMANYAN has estimated that the number of varieties here exceeds 200 out of a world total of 650. Here were also discovered numerous wild wheats, including single-seeded and double-seeded types. In the diversity of species and ecotypes of wheat, this center is the most outstanding of the earth.

[8] In the Caucasus and in Middle Asia the wild species of cherry is not known.

In Asia Minor and in our own Transcaucasia we find the original birthplace of rye, which exists here in amazing diversity of forms, so different from the single variety of rye in Europe. Here we found rye with black and with red spikes and many unusual forms including the new species of wild rye, *Secale vavilovii* Grossh. and *Secale ancestrale* Zhuk.

The world's potential sources of Occidental orchard fruits are concentrated in the Near East, the native home of the grape, pear, cherry, pomegranate, walnut, quince, almond, and fig. *The first orchards were undoubtedly located in the Near East.* In Georgia (SSSR) and Armenia one may still observe all phases of the evolution of fruit growing—from wild groves consisting almost wholly of wild fruit trees, through transitional methods, to methods approaching those of modern fruit growing, including grafting of the better wild varieties on the less valuable wild forms of fruit trees. Here one may see how the farmer, while clearing away forests to make room for grain fields, has left to grow in his fields the better specimens of wild apple, pear, and cherry trees. Recent research has shown that viticultural methods and all of the more important grape varieties have been acquired from the Near East where one can still find wild-growing grapes which are quite suitable for culture in vineyards.

In several genera, such as *Medicago, Pyrus,* and *Amygdalus* and to a considerable degree also in the wheats, species formation has been actively occurring here, and is still going on. For example, natural polyploidy has been discovered here among the wheats and also among numerous species of wild plants, especially those of the alpine and sub-alpine zones.

From Turkey, Persia, and our own regions of Central Asia has come the world's wealth of melons, the possibilities of which have been far from exhausted by modern plant breeders. The leading forage crops—alfalfa, Persian clover, a number of species of *Onobrychis, Trigonella,* vetch, and others have also originated in the Near East.

V. *The Mediterranean Center of Origin of Cultivated Plants.*—The fifth or Mediterranean center is notable for its distinct cultivated plants which are of more limited significance than those from centers previously mentioned.

CEREALS :—

1. *Triticum durum* Desf. subsp. *expansum* Vav., which includes two geographic sections: *mediterraneum* Vav. and *africanum* Vav.—Durum wheat.
2. *Triticum dicoccum* Schrank—(One of the centers) Emmer.
3. *Triticum polonicum* L.—Polish wheat. (One of the centers, localized within narrow limits). Here (in Syria and Northern Palestine) large numbers of wild wheats (*Tr. dicoccoides*) also occur.
4. *Triticum spelta* L.—True spelt. Southern Pyrenees and Tyrol. (Possibly a secondary center).
5. *Avena byzantina* C. Koch—Mediterranean wheat.
6. *Avena brevis* Roth and *A. strigosa* Schreb.—Sand oats. (Pyrenees).
7. *Hordeum sativum* Jess.—Endemic group of coarse-grained barley. (Secondary center).
8. *Phalaris canariensis* L.—Canary grass. (Western Mediterranean).
9. *Ervum monanthos* Desf.—Uniflorous lentil. (Pyrenean Peninsula).
10. *Lens esculenta* Moench subsp. *macrosperma* Bar.—Large-seeded lentil.
11. *Vicia ervilia* Willd.—Bitter vetch. (Eastern Mediterranean, Cyprus, Crete).
12. *Lathyrus sativus macrospermus* Zalk.—Grass pea.
13. *Pisum sativum* L.—Pea. A variety with large seeds.
14. *Vicia faba* var. *major* Harz.—Large-seed beans.
15. *Lupinus albus* L., *L. termis* Forskal, *L. angustifolius* L., *L. luteus* L.—Lupines.
16. *Cicer arietinum* L.—Chick pea. A large-seed group.

FORAGE PLANTS :—

17. *Hedysarum coronarium* L.—French honeysuckle. (Southern part of Apennine Peninsula and Sicily).

18. *Trifolium alexandrinum* L.—Egyptian clover. (Syria and Egypt).
19. *Trifolium repens* L. var. *giganteum*—White clover. (Lombardy).
20. *Trifolium incarnatum* L.—Crimson clover. Cultivated and wild. (Sardinia, Balearic Islands, Algeria, and other regions).
21. *Ulex europaeus* L.—Gorse. (Portugal).
22. *Vicia sativa* L.—Crop vetch. (Wild-growing and cultivated since the time of the Romans; one of the centers).
23. *Lathyrus gorgonii* Parl.—(Syria).
24. *Lathyrus ochrus* DC. Wild (Italy, Spain) and cultivated.
25. *Lathyrus cicera* L. (In cultivation and wild).
26. *Ornithopus sativus* Brot.—Scradella. Wild (Portugal, Spain, Algeria) and in cultivation.
27. *Spergula arvensis* L.—The area of the wild *Spergula* is broader than that of the cultivated.

OIL AND FIBER PLANTS :—

28. *Linum usitatissimum* L. subsp. *mediterraneum* Vav.—Flax. (A variety with large seeds). Also the wild *Linum angustifolium* Huds. in great profusion.
29. *Sinapis alba* L.—White mustard. (Growing wild as a weed and in cultivation; one of the centers).
30. *Brassica napus* L. subsp. *oleifera* Metzg.—Rape.
31. *Brassica nigra* L.—Black mustard. (Main center).
32. *Brassica campestris* L. subsp. *oleifera* Metzg.—Rape. (One of the centers).
33. *Eruca sativa* L.—Rocket salad. (Main center of origin).
34. *Argania sideroxylon* R. and S.—(Morocco).

CULTIVATED FRUITS :—

35. *Olea europaea* L.—Olive.
36. *Ceratonia siliqua* L.—Carob.

VEGETABLES :—

37. *Beta vulgaris* L.—Garden beet. (Found in great diversity of varieties; here is also the wild *Beta maritima* L.).
38. *Brassica oleracea* L.—Cabbage in great variety, also wild; its closely related wild species are: *B. balearica* Pers., *B. insularis* Moris., *B. cretica* Lam.
39. *Petroselinum sativum* L.—Parsley. (In cultivation and wild).
40. *Cynara scolymus* L.—Artichoke. (Wild and in cultivation). A related type is the wild *C. cardunculus* L.
41. *Brassica campestris* L. subvar. *rapifera* Metzg.—Turnip. (Basic center of origin of the European varieties).
42. *Brassica napus* L var. *rapifera* Metzg.—Turnip. (Basic center).
43. *Portulaca oleracea* L.—Purslane. (As a weed and in cultivation; its area extends into Near Asia).
44. *Allium cepa* L.—Onion. Large-size types. (Secondary center).
45. *Allium sativum* L.—Garlic. Large-size forms. (Secondary center).
46. *Allium porrum* L.—Leek.
47. *Allium kurrat* Schweinf.—Chives.
48. *Satureja hortensis* L.—Savory.
49. *Lactuca sativa* L.—Lettuce. The area extends also into Near Asia.
50. *Asparagus officinalis* L.—Asparagus. (The wild varieties are also utilized).
51. *Crambe maritima* L.—Sea kale.
52. *Apium graveolens* L.—Celery. (In cultivation and wild).
53. *Cichorium endivia* L.—Winter endive. (Here is found also its close relative, *C. pumilum* Jacq.).
54. *Cichorium intybus* L.—Chicory. (Growing wild as a weed and in cultivation). Its area is very extensive.
55. *Anthriscus cerefolium* Hoffm.—Chervil. (The area of the wild chervil—(cow-parsley)—also extends into Near Asia).
56. *Lepidium sativum* L.—Cress. (Cultivated and wild; secondary center).
57. *Pastinaca sativa* L.—Parsnip.
58. *Tragopogon porrifolium* L.—Salsify. Wild and in cultivation.
59. *Scorzonera hispanica* L.—Black salsify. Wild and in cultivation. In Spain and Sicily, the wild *S. deliciosa* Guss., is used.
60. *Scolymus hispanicus* L.—Spanish oyster plant. (Wild and cultivated).
61. *Smyrnium olusatrum* L. (In cultivation and wild).—Also as a spice.
62. *Anethum graveolens* L.—Parsley. (Cultivated and wild). Also as a spice.
63. *Rheum officinale* Boill.—Rhubarb.

64. *Ruta graveolens* L.—Garden rue. Also used as a spice.
65. *Rumex acetosa* L. and other species.—Dock.
66. *Blitum rubrum* Rchb., *B. virgatum* L., *B. capitatum* L.

ETHEREAL OIL PLANTS, SPICE PLANTS:—

67. *Nigella sativa* L.—Fennel.
68. *Carum carvi* L.—Caraway.
69. *Cuminum cyminum* L.—Cumin. (Possibly a secondary center).
70. *Pimpinella anisum* L.—Anise. (Cultivated and wild).
71. *Foeniculum vulgare* Mill.—Fennel.
72. *Thymus vulgaris* L.—Thyme.
73. *Hyssopus officinalis* L.—Hyssop.
74. *Lavandula vera* DC.—Lavender.
75. *Mentha piperita* L.—Peppermint.
76. *Rosmarinus officinalis* L.—Rosemary.
77. *Salvia officinalis* L.—Sage.
78. *Iris pallida* Lam.—Iris. (Italy).
79. *Rosa damascena* Mill.—Damask rose.
80. *Laurus nobilis* L.—Laurel.
81. *Humulus lupulus* L.—Hop. In Mediterranean countries mostly wild growing. Its area extends far into the north where it was probably first introduced into cultivation.

PLANTS USED FOR DYES AND TANNING:—

82. *Rubia tinctorum* L.—Madder. Wild and cultivated.
83. *Rhus coriaria* L.—Sumach. Wild and in cultivation (Italy and Spain).

PLANTS USED FOR MISCELLANEOUS PURPOSES:—

84. *Cyperus esculentus* L.—Chufa. (Apparently from Egypt).

This is undoubtedly the native home of the olive and the carob tree, Ceratonia siliqua. A large number of cultivated vegetables, including the beet, have had their origin here. This ranks with China as a center of origin for vegetables. Many of the old varieties of forage plants have originated in the Mediterranean countries. It is interesting to note that each civilization in this center has introduced its own forage plants into cultivation; from Egypt and Syria have come the Egyptian clover; from the Apennines, *Hedysarum coronarium* and *Trifolium repens giganteum;* from the Pyrenees, the single-flowered lentil; from Syria has come *Lathyrus gorgonii;* and from Portugal, the gorse, *Ulex europaeus.* Judging by the species and varieties comprising them, many of the most important cultivated plants, such as wheat and the legumes, indicate the existence, here, of a secondary center of origin, and bear witness to the important role that man has played, since ancient times, in producing improved varieties. *Many of the cultivated plants of the Mediterranean countries, such as flax, barley, beans, and chick pea, are notable for their large seeds and fruits, in contrast to the small-seeded forms of Central Asia, their basic place of origin,* where most of the dominant genes of these plants are concentrated. In all the cultivated plants of the Mediterranean center one can trace the important role played by man in selecting the best cultivated forms.

VI. *The Abyssinian Center of Origin of Cultivated Plants.*— The expedition conducted by us in 1927 in Abyssinia, Eritrea, and Somaliland, and the subsequent comparative study of the large amount of collected material, have established the independence of Ethiopia in its cultivated flora and have proven beyond doubt the existence here (including the hill country of Eritrea) of an independent center of origin of the world's cultivated plants.

CULTIVATED GRAIN CROPS:—

1. *Triticum durum* subsp. *abyssinicum* Vav.—Abyssinian hard wheat. An amazing wealth of forms.
2. *Triticum turgidum* subsp. *abyssinicum* Vav.—Poulard wheat. An exceptional wealth of forms.

3. *Triticum dicoccum* subsp. *abyssinicum* Stol.—Emmer.
4. *Triticum polonicum* L. gr. *abyssinicum* Vav.—Polish wheat.
5. *Hordeum sativum* Jess.—Barley. An exceptional diversity of forms.
6. *Andropogon sorghum* Link.—Grain sorghum.
7. *Eragrostis abyssinica* L.—Teff.
8. *Eleusine coracana* Gaertn. (*E. tocussa* Fresenius).—African millet.
9. *Pennisetum spicatum* L.—Pearl millet. (Grows in semi-arid regions).
10. *Cicer arietinum* L.—Chick pea. (A center).
11. *Lens esculenta* Moench.—Lentil. (A center).[9]
12. *Pisum sativum* L.—Pea. (One of the centers).
13. *Vicia faba* L.—Beans. (Probably a secondary center).
14. *Trigonella foenum graecum* L.—Fenugreek.
15. *Lathyrus sativus* L.—Grass pea. (A center).
16. *Vigna sinensis* Endl. var. *sinensis* (Stick.) Pip.—Cowpea. *V. sinensis* Endl. var. *catjang* (Walp.) Pip.—Catjang.
17. *Dolichos lablab* L.—Hyacinth bean. (A variegated-flowering late variety).
18. *Lupinus termis* Forsk.—Lupine. (Grows in the sands of Northern Abyssinia).
19. *Linum usitatissimum* L.—Flax. Cultivated as a crop for its seeds. (A center).

OIL PLANTS :—

20. *Guizotia abyssinica* Cass.
21. *Carthamus tinctorius* L.—Safflower.
22. *Sesamum indicum* L.—Sesame. (Basic center).
23. *Ricinus communis* L.—Castor bean. (A center).
24. *Lepidium sativum* L.—Garden cress. (Basic center; the greatest diversity of forms is found here).

SPICES AND STIMULANTS :—

25. *Coriandrum sativum* L.—Coriander. One of the centers, a specific group of forms. E. A. STOLETOVA segregates this group into a separate sub-species.
26. *Nigella sativa* L.—Fennel. (A center).
27. *Carum copticum* Benth. and Hook. (A center).
28. *Rhamnus prinoides* Hér.—Buckthorn. (Takes place of hops in the preparation of beer).
29. *Catha edulis* Forsk. (*Celastrus edulis* Vahl.)—Khat. Wild and in cultivation.
30. *Coffea arabica* L.—Coffee.

VEGETABLES :—

31. *Brassica carinata* Al. Braun—Vegetable mustard; this is also an oil plant.
32. *Allium* sp. (*A. ascalonicum* L.)—Onion.
33. *Musa ensete* J. F. Gmel.—Abyssinian banana.
34. *Hibiscus esculentus* L.—Okra. (Mostly wild-growing). Cultivated by Arabs.

PLANTS OF MISCELLANEOUS USES :—

35. *Euphorbia candelabrum* Trem.—Spurge. Wild-growing, used as a hedge plant.
36. *Hagenia abyssinica* Willd.—(Growing only wild).
37. *Commiphora abyssinica* (Berg.) Engler.—Myrrh. (Grows only as a wild plant). Furnishes resin.
38. *Indigofera argente* L.—Indigo. Grows almost entirely as a wild plant. (Cultivated in Egypt and in Arabia).

In spite of the limited agricultural territory, an astonishing wealth of varieties exist here. Barely half a million hectares are under wheat in Abyssinia—an insignificant proportion of the world's total of 160 million hectares. *Yet, according to the number of its botanical varieties of wheat Abyssinia occupies first place.* In fact, botanical, physiological, and genetic studies indicate that the wheats of Abyssinia should actually be divided into separate botanical species. *This is also the center of origin of cultivated barley. Nowhere else does there exist in nature such a diversity of forms and genes of barley. A number of genera of cultivated plants are found only in Abyssinia, for example, the bread grain Eragrostis abyssinica and the oil-bearing Guizotia abyssinica.* Here

[9] Recent studies on the genetics of the lentil (E. I. BARULINA) have shown that the Abyssinian lentil, when crossed with the Afghanistan and Middle-Asiatic forms, remains partly sterile—a fact which proves its individuality.

are found peculiar forms of flax which are used not for their fibers nor for oil but for the flour made from their seeds. In other words, *flax in Abyssinia is a cereal plant.*

The number of plants indigenous in Ethiopia is not large; actually, before the coming of the Europeans, Ethiopia knew nothing of fruits or vegetables. This is primarily a land of field crops which exist in amazing diversity of varieties; it is surprising that this diversity expresses itself under relatively uniform ecological conditions, since the region of cultivated plants here is concentrated in high alpine regions, 1500 to 2500 meters above sea level.

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We have now examined all the primary centers of origin of plant forms in the Old World. Studies based on our expeditions, conducted by the Institute of Plant Industry from 1925 to 1933, have shown that the New World is characterized by a very distinct localization of its basic centers of origin of plant forms. These centers are restricted to Central America and comprise southern Mexico and the central part of the South American Andes, including Ecuador, Peru, and Bolivia. Here we find two independent centers: the Central-American, including southern Mexico, and the Andes center, comprising the present territories of Peru, Bolivia, and Ecuador.

In the limited territory embracing the southern sections of Mexico, Guatemala, Honduras and a part of Costa Rica, originated the cultivated plant resources of the New World.

VII. *The South Mexican and Central American Center of Origin of Cultivated Plants* (Including the Antilles).

CROP CULTURES:—

1. *Zea mays* L.—Corn.
2. *Phaseolus vulgaris* (L.) Savi—Common bean.
3. *Phaseolus multiflorus* Willd.—Multiflorous bean.
4. *Phaseolus lunatus* L. gr. *microspermus*—Lima bean.
5. *Phaseolus acutifolius* A. Gray var. *latifolius* Freeman.—Tepary bean.
6. *Canavalia ensiformis* DC. (?)—Jack bean.
7. *Chenopodium nuttalliae* Saff., *Ch. ambrosioides* L.—American wormseed.
8. *Amarantus paniculatus* L. var. *leucocarpus* Saff.—Tassel flower.

MELON PLANTS:—

9. *Cucurbita ficifolia* Bouche (*C. melanosperma* Al. Braun).—Malabar gourd.
10. *Cucurbita moschata* Duch.—Winter crookneck pumpkin.
11. *Cucurbita mixta* Pang.
12. *Sechium edule* Swartz.—Chayote.
13. *Polakowskia tacaco* Pittier. (Costa Rica).
14. *Sicana odorifera* Naud.—Curuba.

THICKENED TAPROOTS AND ROOT TUBERS:—

15. *Pachyrrhizus tuberosus* Spreng. (*Cacara edulis* Kuntze).—Yam bean.
16. *Ipomoea batatas* Poiret.—Sweet potato.
17. *Maranta arundinacea* L.—Arrowroot. (Antilles).

SPICE PLANTS:—

18. *Capsicum annuum* L.—Pepper.
19. *Capsicum frutescens* Will.—Pepper.

FIBER PLANTS:—

20. *Gossypium hirsutum* L.—Upland cotton.
21. *Gossypium purpurascens* Poir.—Bourbon cotton.
22. *Agave sisalana* Perrine—Sisal hemp. *Ag. ixtli* Karw.—Henequen.

FRUITS:—

23. *Opuntia* sp.—A number of species.—Prickly pear.

24. *Anona cherimolia* Mill. (Possibly a secondary center). *A. reticulata* L., *A. squamosa* L., *A. muricata* L., *A. purpurea* Moc. and Sesse, *A. cinerea* Dun., *A. diversifolia* Safford, *A. glabra* L.
25. *Sapota achras* Miller, *Sapota sapotilla* Coville.—Sapodilla.
26. *Casimiroa edulis* La Llave.—White sapote.
27. *Calocarpum mammosum* (L.) Pierre.
28. *Calocarpum viride* Pittier (*Achradelpha viridis* Cook).
29. *Lucuma salicifolia* H. B. K.—Yellow sapote.
30. *Carica papaya* L.—Papaya.
31. *Persea schiedeana* Nees and *P. americana* Mill. (*P. gratissima* Gaertn.)—Avocado.
32. *Psidium guayava* L.—Guava.
33. *Psidium friedrichsthalianum* (Berg) Niedenzu, *P. sartorianum* (Berg) Niedenzu.—Guava.
34. *Spondias mombin* L.—Yellow mombin. *S. purpurea* L.—Purple mombin.
35. *Crataegus mexicana* Moc. and Sesse, *C. stipulosa* Steud.—Hawthorns.
36. *Diospyros ebenaster* Retz.—Black sapote.
37. *Chrysophyllum cainito* L.—Star apple. Found chiefly on the Antilles Islands, in Jamaica, in Panama, both in wild and cultivated form.
38. *Anacardium occidentale* L.—Cashew. Antilles, Panama.
39. *Prunus serotina* Ehrhart (*Pr. capollin* DC).—Wild black cherry. (Mostly wild).

MISCELLANEOUS CULTIVATED PLANTS:—

40. *Agave atrovirens* Karw.—Agave.
41. *Cereus* sp.—Cacti. Used for hedges.
42. *Nopalea coccinellifera* Mill.—Cochineal plant.
43. *Tigridia pavonia* Ker-Gawl—Tiger flower. (Mostly wild-growing).
44. *Physalis aequata* Jacq.—Mexican tomato.
45. *Lycopersicum cerasiforme* Dun.—Cherry tomato.
46. *Salvia chia* Fernald—An oil plant.
47. *Theobroma cacao* L.—Cacao.
48. *Bixa orellana* L.—Annatto. A dye and spice plant.
49. *Nicotiana rustica* L.

The use of the phytogeographic method has shown clearly that this is *the primary center of corn (maize) and its most closely related wild species, teosinte. This center is also the native home of the chief American species of bean, squash, pepper, and numerous tropical fruits. Here the cultivation of cacao had its origin; this is probably also the home of the sweet potato. Upland cotton, the variety upon which the cotton growing of the world is based, had its origin in southern Mexico.* Here maize has played a role similar to that of wheat in the centers of origin of the Old World. Without it, the Maya civilization could have never existed. The very restricted territory of southern Mexico and Central America is full of cultivated endemic plant varieties, differing strikingly, in this respect, from the vast North American continent where all agriculture, both past and present, is based upon imported varieties.

* * * * *

Our investigations in South America, conducted in 1932 and 1933, have compelled us to make important corrections in the former conceptions of centers of origin as recorded in American literature. The most outstanding region, which was undoubtedly a center of independent and original agriculture, is the high mountainous area of Peru, Bolivia, and part of Ecuador, which was formerly the center of the so-called Megalithic or Pre-Inca civilization. This territory, insignificant in area as compared with South America, is remarkable for its collection of cultivated endemic animals and plants.

VIII. *South American (Peruvian-Ecuadorean-Bolivian) Center of Origin of Cultivated Plants* (the chief endemic plants of the high mountainous districts—Puna and Sierra).

ROOT TUBERS :—

1. *Solanum andigenum* Juz. et Buk.—Potatoes from the Andes, most widely distributed between Bolivia and Central America (chromosome number 2 x 48).
2. Other endemic potato species (cultivated):
   S. cuencanum Juz. and Buk.—Ecuador. (24 chromosomes).
   S. kesselbrenneri Juz. and Buk.—Ecuador. (24 chromosomes).
   S. ajanhuiri Juz. and Buk.—Bolivia. (24 chromosomes).
   S. pauciflorum Juz. and Buk.—Bolivia. (24 chromosomes).
   S. stenotomum Juz. and Buk.—Bolivia, Peru, Ecuador. (24 chromosomes).
   S. goniocalyx Juz. and Buk.—Peru. (24 chromosomes).
   S. rybinii Juz. and Buk.—Colombia. (24 chromosomes).
   S. bayacense Juz. and Buk.—Colombia. (24 chromosomes).
   S. juzepczukii Buk.—Peru and Bolivia. (36 chromosomes).
   S. tenuifilamentum Juz. and Buk.—Peru and Bolivia. (36 chromosomes).
   S. mamilliferum Juz. and Buk.—Peru. (36 chromosomes).
   S. chocclo Juz. and Buk.—Peru, Bolivia, Ecuador. (36 chromosomes).
   S. riobambense Juz. and Buk.—Ecuador. (36 chromosomes).
   S. curtilobum Juz. and Buk.—Peru and Bolivia. (60 chromosomes).
3. *Oxalis tuberosa* Molina, *O. crenata* Jack.—Oka.
4. *Tropaeolum tuberosum* Ruiz and Pav.—Edible nasturtium.
5. *Ullucus tuberosus* Lozano.—Ulluco.

CULTIVATED CROPS :—

6. *Lupinus mutabilis* Sweet—Bolivian lupine.
7. *Chenopodium quinoa* Willd —Quinoa.
8. *Chenopodium canahua* (Indigenous to higher elevations in Bolivia and Peru).
9. *Amarantus caudatus* L.—Tassel flower.
10. *Lepidium meyenii* Walp.

Plants endemic to irrigated coastal regions of Peru and non-irrigated subtropical and tropical regions of Ecuador, Peru and Bolivia.

(Bearing the ecological names: costa, ceja, yunga, montana).

CULTIVATED CROPS :—

11. *Zea mays* L. gr. *amylacea*—Starchy maize, large-grained forms. (Secondary center of varieties).
12. *Phaseolus lunatus* L. gr. *macrospermus*—Lima bean. (Secondary center).
13. *Phaseolus vulgaris* L.—Common bean. (Secondary center).

ROOT TUBERS AND THICKENED TAPROOTS :—

14. *Solanum phureja* Juz. and Buk.—Potato, Bolivia. (24 chrom.).
15. *Polymnia sonchifolia* Poepp. and Endl.
16. *Xanthosoma sagittifolium* Schott (*X. edule* Meyer).—Malanga.
17. *Canna edulis* Ker-Gawl.—Edible canna.
18. *Arracacia xanthorrhiza* Bancroft (*A. esculenta* DC.)—Apio.

VEGETABLES :—

19. *Solanum muricatum* Ait.—Pepino.
20. *Lycopersicum esculentum* Mill. var. *succenturiatum* Pasq.; *L. peruvianum* Mill.—Tomato.
21. *Cyclanthera pedata* Schrader, *C. brachybotrys* Cogn.
22. *Cyphomandra betacea* Sendtn.—Tree tomato.
23. *Physalis peruviana* L.—Ground cherry.

SQUASH PLANTS :—

24. *Cucurbita maxima* Duch.—Pumpkin. (Probably taken from the eastern slopes of the Cordilleras).

SPICES AND STIMULANTS :—

25. *Capsicum frutescens* L. var. *baccatum* L.; also *C. pubescens* Ruiz and Pav.—Pepper.
26. *Tagetes minuta* L.—Marigold.
27. *Erythroxylon coca* Lam.—Cocaine bush.
28. *Bixa orellana* L.—Annatto. (Secondary center).

FIBER PLANTS :—

29. *Gossypium barbadense* L. (*G. peruvianum* Cav.)—Egyptian cotton.
30. *Fourcroya cubensis* Vent.

FRUIT CROPS :—

31. *Passiflora ligularis* Juss.; *P. quadrangularis* L.—Passion-flower.
32. *Carica candamarcensis* Hook., *C. chrysopetala* Heilborn, *C. pentagona* Heilborn—three Ecuadorean species; *C. pubescens* (A. DC.) Solms Laub. and *C. candicans* A. Gray—two Peruvian species.
33. *Lucuma obovata* H. B. & K., *L. caimito* A.c.X.C.—Wild and cultivated.
34. *Psidium guajava* L.—Guava. Wild and cultivated.
35. *Anona cherimolia* Mill. (One of the centers).
36. *Inga feuillei* DC.
37. *Bunchosia armeniaca* DC.
38. *Matisia cordata* Humb. & Bonpl.
39. *Caryocar amygdaliferum* Cav.
40. *Guilielma speciosa* Mart.—Peach palm.
41. *Malpighia glabra* L.—Barbados cherry.
42. *Solanum quitoense* Lam.
43. *Prunus capuli* Cavanille (*Pr. capollin* Zucc.)—Capollin. Differs from the Central-American group; mostly wild-growing.

MEDICINAL PLANTS :—

44. *Cinchona calisaya* Wedd., *C. succirubra* Pav.—Quinine tree. (Mostly wild-growing).
45. *Nicotiana tabacum* L.—Tobacco (?). According to recent genetic investigations (D. Kostov and others), the common tobacco may have arisen from a cross of the wild *N. sylvestris* and *N. rusbyi* or other Andean species closely related to these with subsequent doubling of the chromosomes (amphidiploidy) which made this inter-specific hybrid fertile.

Soviet expeditions have discovered in this 8th center of plant origin enormous and almost untapped resources of cultivated plants. They found dozens of new species of potatoes, some cultivated and other closely related wild forms, all of which were used as food by Indian tribes. *The high mountains of Peru, Bolivia, and Ecuador are full of endemic species, from unusual sorts of potatoes to rare tuber plants found at present only in this part of the globe, such as Oxalis tuberosa, Tropaeolum tuberosum, and Ullucus tuberosus.* The cultivated grain crops, produced here include such unusual species as *Chenopodium canahua* and others. There exist here not only cultivated endemic plants but also unusual endemic animal types indigenous to Peru and Bolivia (the llama and the alpaca). Both the animals and the plants are concentrated chiefly in the so-called "punas"—plateau prairies at an altitude of 3500-4300 meters. The crops are grown here without irrigation. Even at present, one may see transition stages from cultivated plants to the wild ones. There is no doubt that both plant and animal husbandry in South America has had its start in the "puna." The localization of endemic species of cultivated plants and animals is very distinct and restricted in the present as it has been in the past.

The coastal regions of Peru which were populated later, during the Inca civilization, present a striking ecological contrast to the high mountain regions. The former are mostly desert and plant cultivation is possible only by the aid of irrigation. The agriculture of the Incas, remarkable though it is, is undoubtedly of secondary origin, just as the Egyptian agriculture. Both Egyptian and the Inca agriculture were based on artificial irrigation. Before the advent of the farmer, there was no original wild flora; there was neither corn nor cotton in Peru. Most of the plants of the irrigated regions of Peru were imported from Central America or from the Eastern slopes of the Cordilleras where one still finds growing wild in the forests such endemic species as the cinchona tree and the cocaine shrub.

It is necessary to add to the basic Peruvian center of plant origin the territory of the small island of Chiloe, located near the shore of southern Chile. It was here that the Europeans obtained from the Indians the Irish potato, *Solanum tuberosum,* as well as the *S. andigenum,* a variety which also possesses

48 chromosomes and closely resembles the Irish potato morphologically. This variety is particularly suitable for European conditions because it is adapted to long periods of daylight. Most of the species and forms of the potato from Peru, Bolivia and Ecuador require a short day for their normal development, and under usual European conditions, with long days during the summer months, these varieties fail to produce tubers.

VIII*a*. *The Chiloe Center of Origin of Cultivated Plants.*

1. *Solanum tuberosum* L.—Common potato. (48 chromosomes).
2. *Madia sativa* Molina—Chile tarweed. An oil plant.
3. *Bromus mango* Desv.—Chilean center of origin (Extinct).
4. *Fragaria chiloensis* Duchesne—A wild growing strawberry.

The enormous territory of Brazil with its rich flora, estimated by botanists (HOEHNE) to comprise 40,000 species, up to the present has furnished the world with a very insignificant number of cultivated plants, of which the most important are manioc, peanut, and pineapple. It is interesting to note that even these plants are indigenous not to moist tropical forests but to the semiarid regions of Brazil. The rubber tree still grows wild in its native home, the valley of the Amazon river, whence it has been introduced into southern Asia by the Dutch and English during the past decades.

VIII*b*. *Brazilian-Paraguayan Center of Origin of Cultivated Plants.*

ENDEMIC PLANTS:—

1. *Manihot utilissima* Pohl.—Manioc. (Growing on light dry soils).
2. *Arachis hypogaea* L.—Peanut. (On light soils).
3. *Phaseolus caracalla* L.—Snail flower.
4. *Theobroma cacao* L. (Secondary center), *T. grandiflora* K. Schum. (*Guazuma grandiflora* G. Don.) and other species.—Cacao. (Valley of the Amazon river).
5. *Hevea brasiliensis* Müll.—Rubber tree. (Valley of the Amazon river).
6. *Ilex paraguayensis* A. St. Hil.—Paraguayan tea.

CULTIVATED FRUITS:—

7. *Eugenia uniflora* L.—Surinam cherry. *E. uvalha* Cambess.; *E. dombeyi* Skeels—Grumixameira tree; *E. tomentosa* Cambess.—(All of these are cultivated).
8. *Myrciaria jaboticaba* Berg.; *M. cauliflora* Berg.—Jaboticaba.
9. *Ananas comosa* (L.) Merr.—Pineapple. (On dry soils).
10. *Bertholletia excelsa* Humb. and Bonpl.—Brazil nut. (Growing wild).
11. *Anacardium occidentale* L.—Cashew. (Also growing on the Antilles).
12. *Feijoa sellowiana* Berg.
13. *Passiflora edulis* Sims—Purple granadilla.

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Still later, although before the time of COLUMBUS, the Indians introduced and cultivated the Jerusalem artichoke and the sunflower in the northern region of the present United States, where these plants are still found growing wild.

These are the localities of concentration of the world's sources of the principal cultivated plant species and varieties, as determined by detailed phytogeographic investigations of the last decade. More exact information will probably be necessary in the case of a number of tropical plants growing in adjacent centers. The centers of primary origin for plants which are economically most interesting to the SSSR have been established quite accurately. All these centers undoubtedly have developed independently from each other, which is borne out by the composition of the genera, species, and varieties of cultivated plants, as well as by their distinctive agricultural methods, implements, and domesticated animals.[10]

[10] See N. VAVILOV: *World centers of animal and plant breeding.* Proceedings of the second All-Union Conference on the evolution of domestic animals at the Academy of Sciences SSSR (1934).

It is important to note that the eight basic centers are separated by deserts or by mountain ranges. The Chinese center is separated from the Central Asiatic center by an enormous desert and by the semi-desert plateaus of Central Asia. The Near Eastern center is isolated from the Central Asiatic center by the desert of eastern Afghanistan and the Bakvian and Seistan deserts of western and central Iran. From India proper, the Central Asiatic center is separated by the Tar desert. The Mediterranean center is bounded by deserts on the east and south. Similarly, Abyssinia is encompassed by deserts. The high mountainous region of Peru and Bolivia which was the cradle of agriculture in South America is bordered by the desert of Atacama on the west. North of Southern Mexico are located the Mexican desert plateaus. Indeed, the very geography of the primary centers of origin isolates them, and thus has contributed to the independent development of the floras and human population, the interaction of which has brought about the independent agricultural civilizations. The deserts were formidable obstacles to the primitive peoples, keeping them isolated for long periods.

The foregoing lists comprise the most important cultivated plants of the world. Outside these primary centers there have been few plants introduced into cultivation, and some of these, especially forage plants, vegetables, and medicinal plants, have been only recently introduced. Among important crop plants of ancient cultivation outside these centers are the date palm (probably from the oases of Mesopotamia and northwest India and possibly independently also from Africa), and the watermelon which is found growing wild in the desert and semi-desert regions of South Africa.

Differential maps of the geographic localization of varieties showing places of concentration of the maximum number of original plant varieties have been compiled on the basis of the enormous amount of seed and seedling material collected by the expeditions of the Institute of Plant Industry (about 300,000 samples). Cultivated plants which are of greatest importance to the SSSR have been planted and studied in detail. Such maps have been compiled for varieties of wheat, oats, barley, rye, corn, millet, and flax; of the legumes, for peas, lentils, beans, chick peas, grass peas, and mung beans; of vegetables for carrots and tomatoes as well as for root crops and potatoes (see N. Vavilov: *Centers of Origin of Cultivated Plants,* also articles on separate cultivated plants published in "Trudi po Prikl. Bot., Gen. i Sel." (1923-1934).

On the whole, it appears clear that the primary regions of formation of the most important cultivated plants are localized within very narrow limits, occupying approximately 1/40th of the entire dry land area of the earth (not including desert and rocky sections within the areas of the centers proper). From the lists given above it seems apparent that an overwhelming majority of cultivated plants had their origin in the Old World. Of the 640 most important cultivated plants listed, over 500 belong to the Old World, *i.e.*, 5/6 of the cultivated plants of the world. The New World contributed approximately 100 plants (considering each newly discovered species of the potato as a separate plant). *Within the limits of the Old World, the greatest number of cultivated plants had their origin in southern Asia—over 400 plants or almost 2/3 of all the crop plants under cultivation.* If the calculation were based on the exact number of species, the number of plants would be larger but the proportions would remain the same. The greatest potential resource of species and varieties of cultivated plants is located in the mountains and tropical regions of southern Asia. The smallest number of plants is found in Africa which has contributed only 50 cultivated plants. Australia knew nothing of cultivated plants until recent times. Some of the members of its wild flora have been introduced into

cultivation only during the 19th century: such are, for example, the eucalyptus, acacia, and cassowary.

An unusual wealth of original genera, species, and varieties of plants is found in India and China, countries which have contributed almost half of our crop plants; large original floras exist also in the Near East and the Mediterranean countries.

If, besides the cultivated plants, one takes into account also the wild varieties which are utilized by inhabitants of these countries, one can understand the material basis on which the enormous agricultural populations in these territories have subsisted in the past and are still destined to live.

The actual location of the primary plant cultures is more clear and distinct than it appeared to be in the times of DE CANDOLLE (1882), whose main concern was with whole continents. A concrete study of plant resources by the differential method has permitted the exact delimination of the basic regions of formation of cultivated plants within the continents.

We have presented here only a summary of data concerning the most important species found within the limits of the larger centers; one could continue to make further geographic differentiation within the regions mentioned. In the case of many species of economic importance to Soviet agriculture, with an exactness that is exceptional in botanical investigations, we have succeeded in establishing locations of the centers of their origin within radii of a few hundreds of kilometers in many cases.

The method of phytogeographic differential plant study has fully justified itself. Using it we have disclosed enormous resources of species and varieties of cultivated plants and their most closely related wild forms—resources which no botanist or agronomist has ever suspected in the past. *In a great many cases of our most important cultivated plants, we have had to reconstruct our entire conception of the species and their composition.*

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The enormous quantity of field and vegetable crop material discovered in these centers should be widely used in breeding work in the SSSR.

It is clear that the zone of initial development of the most important cultivated plants lies in the strip between 20° and 45° north latitude, near the higher mountain ranges, the Himalayas, the Hindu Kush, those of the Near East, the Balkans, and the Apennines. In the Old World this strip follows the latitudes while in the New World it runs longitudinally, in both cases conforming to the general direction of the great mountain ranges.

The plant lists given above for the separate centers show another very important fact, namely, that a number of plants have had their origin in several regions or centers. Of these plants a different Linnaean species may be indigenous to each center, the difference showing clearly physiologically and in the number of chromosomes. This is very clear in the cases of wheat, potato, oats, cotton, fruit trees. Data obtained by the differential phytogeographical method have revealed that DE CANDOLLE's old opinion that the native home of wheat is Mesopotamia, and the statement of the famous Austrian geobotanist, SOLMS-LAUBACH, that the birthplace of wheat was in Central Asia, have no foundation. The case of wheat and oats is a good example of the complicated picture of distribution of the basic potential of a plant. Whereas the original common wheat species (42 chromosomes) are centered between Hindu Kush and the western Himalayas and also in Transcaucasia, species having 28 chromosomes are concentrated in Abyssinia or in the Near East (Transcaucasia, Turkey, northwestern Iran) which is a region of endemic wheat species and

their closely related genera. These facts have enabled us to exercise control over original material for breeding. They have shed entirely new light on the problem of source materials for the most important cultivated plants. Among the newly discovered plant sources we have found many valuable agronomic properties such as resistance to diseases and awnlessness in some wild hard wheat varieties found in Abyssinia. In the mountainous regions of Peru and Bolivia there were found certain species of potato which have been able to withstand temperatures as low as —8° C. These facts have proven to be so significant that, after the Soviet expeditions, special expeditions were sent from Washington, from Sweden, and from Germany into Central and South America. The most recent German expedition went to India with one definite object—"to collect wheat materials in this world geographic center of soft wheat genes."[11]

Even if we consider as completed the investigation of the world's resources of certain crop plants such as wheat, barley and legumes, there still remains an enormous amount of work to be done on vegetables and cultivated fruits. We can look forward to important discoveries on fruits in China, Asia Minor, and Iran. Of great interest would be a thorough exploration of northwestern India where the most important European field crops have had their origin.

5. **Primary and Secondary Crops:**— Our research has suggested a division of all cultivated herbaceous plants into two groups. The first group consists of plants cultivated from ancient times and known only in cultivation or in wild state. These we called the primary group. To this group belong such plants as wheat, barley, corn, soy bean, flax, and cotton.

The second group consists of all plants which have been derived from weeds which grew among the basic primary plants.

We have determined that cultivated rye has arisen from rye which grew as a weed in fields of wheat and winter barley in southwestern Asia and Transcaucasia where it is now found in great diversity in its weed form. In Afghanistan, rye is a stubborn weed, especially since many of its forms have a tendency to self-sowing (shattering).

With the northward movement of cultivated wheat and winter barley from southwestern Asia—from the basic center of formation of soft wheats into Europe and Siberia—rye began to replace wheat. Due to its winter hardiness and its general tolerance of soil conditions, rye replaced wheat, with man's assistance, and became an independent cultivated crop as may be observed at present in mountainous regions of southwestern Asia and also in our own country, in North Caucasus.

The predominance of rye which is found in the northern European areas of Soviet Russia and in northern Germany is largely a result of natural selection. At the northern edge of the zone of wheat adaptation, the farmer often plants a mixture of rye and wheat, since such a mixture guarantees him a better yield than wheat alone, which is likely to freeze out in cold winters. We were able to clarify the entire process of replacement of wheat by rye to the minutest detail.[12] Evidently it was wheat that brought rye into cultivation; it is impossible to understand the origin of cultivated rye without cultivated wheat. An important fact for breeding is the presence of a large source of the genes of rye among the weed varieties of rye in southwestern Asia.

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[11] This was the official designation of this expedition. (We are quoting from a letter of Dr. Rudorf.)

[12] See Vavilov, N. Centers of origin of cultivated plants. Trudi po Prikl. Bot. 16(2), 1926.

Thus, in our search for new genes and for new valuable characters, we have had to resort to a weed found in wheat fields.

A similar situation, but one even more complicated, was found in the case of oats. It is interesting that the various forms of oats, differing in their chromosome number, are associated, in their origin, with the separate geographic groups of emmer and of barley. As the ancient cultivated forms of emmer moved northward, the weed oats which grew in fields of cultivated wheat replaced the wheat and became an independent crop. In seeking new forms, new genes of oats, the breeder should give special attention to the centers of origin of the ancient forms of cultivated emmer, for it is in these centers that he will find a great diversity of original genes of cultivated oats.

Similar facts have come to light in connection with a number of other plants, such as *Eruca sativa,* certain mustards, rape, and other crucifers, the coriander, a number of potato varieties of Peru and Bolivia, and the Peruvian tomato. A study of weeds growing in cultivated fields should open new possibilities for breeding from this point of view.

6. **Regularities in the Geographic Distribution of Varietal Diversity of Cultivated Plants:**— The accumulation of a large number of facts on the distribution of varieties in the primary centers and on the migration of these varieties from the original centers has disclosed a number of important principles which facilitate our search for necessary and valuable material.

We have already mentioned the fact that on the periphery of the areas occupied by a given plant and in places of natural isolation, such as islands and isolated mountain regions, one may often find extremely interesting original recessive forms which are the result of inbreeding or of the process of mutation. We have a very large number of such cases. China, for instance, is characterized by the presence of peculiar cultivated plant forms of secondary origin, introduced from their primary centers of origin. Here we find the world's greatest diversity of varieties of hull-less barley (smoothness of grain is a typically recessive character), also of hull-less millet and of large-seeded hull-less oats (*Avena nuda*). Here also, as we have previously stated, we find segregations of peculiar recessive forms of waxy corn and of asparagus bean. The latter is a variety lacking the parchment layer in the wall of the bean pod, which makes the beans edible in the pod. It is possible that these recessive qualities have been brought out by intensive breeding conducted since ancient times by primitive Chinese breeders.

Unusual eligulate forms of rye, of soft wheat, and of club wheat are restricted to the region of Palmyra, growing in isolated regions of Badakhshan and Shugnan and in the mountainous regions of Soviet Tadjikistan and of Afghan Tadjikistan. Varieties of hard eligulate wheat were found segregated in the place of their origin, on the island of Cyprus.

It is possible to trace remarkable geographic regularities in the distribution of cultivated plants from the Himalayas to the Mediterranean Sea. The group of mountain ranges between the Himalayas and Hindu Kush offers the world a collection of astounding wealth of primitive, mostly dominant forms of peas, beans, chick peas, and grass peas with small seeds and pods. The varieties of *Lathyrus* found in Palmyra and in northwest India are characterized by having blue, often very dark blue, flowers and dark, small speckled seeds. As we move westward to Iran we find larger forms, recessive forms, forms with white seeds and with pink flowers. Countries around the Mediterranean have almost none but very highly cultivated forms with large white seeds and white flowers.

We find the same phenomenon in the case of the lentil which is represented

at Chitral and on the boundary between India and Afghanistan by black small seeded forms differing from the large seeded forms of the Mediterranean. The bean seeds of Sicily and Spain are seven or eight times larger than those growing in the region of Kabul (Afghanistan) and in Badakhshan. The same is true of the chick pea. The Mediterranean area is also characterized by its large-seeded forms of flax, wheat, and barley. In Algeria we found varieties of the onion with bulbs weighing up to 2 kilograms each.

Thus we see that in a number of species the recessive characters increase as we go from the Himalayas to the Mediterranean, and that the seeds and fruits become larger, a fact which is very important to keep in mind when searching for the most valuable forms.

We also have observed certain regularities with respect to immunity from disease. Certain geographic groups are generally resistant to specialized types of smut, rust, mildew, and other parasitic fungi and also to bacterial diseases. The American group of species of grapes, for example, is characterized by its resistance to *Phylloxera* and to mildew. The East Asiatic species of apple, pear, and chestnut are strikingly different in their reaction to disease from our West Asiatic and European cultivated species and varieties. The sesames of Abyssinia, southwestern Asia, India, and Japan differ greatly from each other in their reactions to the same bacterial infections. The hard wheats of the Mediterranean countries possess a distinct immunity from stripe and leaf rusts in contrast to the relatively susceptible hard wheats of Abyssinia and partly of Egypt. The *dicoccum* types of different geographic regions are quite distinct in the degree of their immunity from the stripe, leaf, and stem rusts and from mildew. These varieties range in their reaction to mildew and the rusts from complete immunity to great susceptibility.

Very interesting regularities have been discovered in the study of varietal material from Yemen in the mountainous regions of Arabia. In this country, adjoining the desert of Arabia, with its peculiar climatic conditions, there have evolved very early-maturing types of all herbaceous crops grown in the mountains. Here we find the most early-maturing wheats of the world. The same is true for varieties of barley, lentil, and fenugreek. We also found that the blue Arabian alfalfa matures very early, its vegetative period being almost as short as that of the annual alfalfa.

The different geographic groups are also characterized by other biological differences. For example, the grass pea forms of Afghanistan, Palmyra, and Tadjikistan have a tendency to self-pollinate, while the European Mediterranean forms show, on the contrary, a tendency toward cross-pollination. The boreal forms of forage grasses have a tendency toward apogamy, a fact which has a decisive influence on methods of breeding.

In beginning his work with different plant groups, the breeder must take into consideration the phytogeographic peculiarities of the species with which he is concerned. This will help him with his practical problems by enabling him to find the most suitable original materials for his purposes.

7. **The Finding of Valuable Forms Far Removed from Primary Centers of Origin:**— In exploratory work one often comes upon exceptionally valuable forms far from the primary centers of their origin. Thus, for instance, the well known variety of orange, the "Washington Navel," was discovered in Brazil, whereas the basic center of citrus fruits is located in southeastern Asia. At present, enormous plantations in the United States are devoted to the growth of this variety which apparently originated as a mutant form or accidental seedling in Brazil. The famous Jaffa oranges probably had

their origin in a bud mutation found in Palestine. To the same category belong some of the curious recessive forms of secondary origin of cultivated plants growing in China.

There is no question that the results of deliberate breeding work of the past centuries and decades represent an enormous achievement. The use of such breeding stocks may greatly facilitate the work of practical breeding.

8. **Original Forage Plant Materials:**— Only two of the existing centers of origin of plants possess endemic groups of cultivated forage plants, namely, the Near Eastern and the Mediterranean centers. These centers have given rise to a number of highly valuable plants such as alfalfa, a number of clovers, grass pea, lentil, vetch, seradella, and French honeysuckle. The same centers have long been known to have domesticated our most important animals and to have developed the science of animal husbandry.[18] The introduction of forage plants into cultivation has originated at a relatively late period, dating but a few centuries back. In the case of most of the basic cultivated plants, we must seek the primary sources of their origin in our search for new varieties; but in the case of forage plants, we already have an enormous supply of species and varieties in our native vegetation. Actually, the breeder has just entered the stage of selection among species, to say nothing of varieties.

Research all over the world during recent decades points to the great importance of the European and Siberian native flora as original material for the breeding of new forage plants. It is interesting to note that the American flora which has been quite well studied and frequently used in introducing new plants into cultivation (MALTE and KIRK in Canada; PIPER, HITCHCOCK and others in the United States) has rarely shown species which were able to compete with the European forage plants. Only one Canadian species, *Agropyrum tenerum* Vasey, deserves special mention; however, it occupies but very limited areas in North America and is of interest to us only for certain regions of western Siberia. A great number of species of grasses and of annual and perennial leguminous plants of our Union deserve serious consideration as original materials for introduction into cultivation. The Swedish expedition headed by TURESSON, conducted in 1928, in western Siberia and in Altai, disclosed the following interesting fact: Apparently certain plants of foothill regions of Altai and of western Siberia, which possess a double chromosome complex, are characterized by rapid growth and by large vegetative bulk as compared to related species growing in northern Europe. According to the Swedish scientists, certain western Siberian species deserve special consideration for breeding because they surpass the forage plants originating from the local varieties of northern Europe.

In order to supply the breeder with the best available material, one must possess a broad geographic outlook with the ability to utilize varied ecogeographical groups within the limits of a given species. One should make the most of mountainous regions, especially Caucasus which is so rich in forms of alfalfa, sainfoin, vetch, *Lathyrus,* and forage grasses. The expeditions of the Institute of Plant Industry and of the Institute of Forage Plants have collected during recent years over 250 species of wild forage grasses represented by many specimens, all gathered within the limits of the SSSR. These are now being grown in special seed plots and studied to determine the most valuable species and ecological types. Usually there is found a great diversity of eco-

[18] VAVILOV, N. I. "World Centers of Animal and Plant Breeding." Paper presented at the Second All-Union Conference on the Evolution of Domestic Animals at the Academy of Sciences, March 1934.

geographic forms within the limits of each species. To select from this diversity of forms is the basic problem of the plant breeder. As illustrated in the breeding of red clover, the correct geographic approach in selecting original breeding material determines the success or failure of the selection (P. I. Lisitzin).

9. **The Theory of Climatic Analogies in Plant Introductions:**— In selecting species and varieties for the SSSR one has to take into account the climatic conditions under which the plants introduced were growing and whenever possible, to select varieties from regions more or less similar climatically to our country. The knowledge of the climate of the country from which the original material for breeding has been collected is very important.

However, it must be borne in mind that the question of climatic analogy cannot be disposed of as readily as it has been in the recent past. A study of the distribution of plants shows the complex nature of this process.

Some cultivated plant varieties possess a surprising universality. This is true for many forage grasses and cultivated vegetables. Denmark exports seeds of vegetables into many countries of the world. According to the data of the seed-testing laboratories of the SSSR, the Danish vegetable seeds are found best for our own regions although our climatic conditions are very different from those of Denmark. We use these Danish seeds throughout the entire Union and even beyond the Arctic circle. Southern Sweden exports forage grass seeds all over the world. The Swedish oats, "Conquest," has truly conquered the entire world; it is successful in our western Siberia and in the Ukraine, as well as in western Europe, under the most varied climatic and soil conditions. The Pettkover rye, bred in northern Germany, is cultivated with success throughout all Germany as well as in our own country. Many herbaceous ornamentals are also surprisingly universal. Petunias, fuchsias, snapdragons, lobelia, mignonette, nasturtium, dahlias, asters, stocks, and many others are grown from seed all the way to the Arctic Ocean, in spite of their tropical and subtropical origin. In other words, some plants and plant varieties seem to be cosmopolitan under cultivation.

On the other hand, the majority of imported varieties of spring and winter wheat and barley are of little interest to us even when transplanted into very similar conditions. The best standard varieties of the world planted over immense areas in Canada and the United States, such as Marquis wheat, are not adapted to areas of any size in the SSSR and are, therefore, less desirable than our own varieties. Many varieties of this group of plants are found to be thus *specialized;* however, there are exceptions even among such plants.

For example, the Saratov wheat variety "Lutescens 062" was unexpectedly found suitable for the coastal region of the Far East, where the climatic conditions bear very little resemblance to those of Saratov. The Australian summer wheat, Aurora, grows well in Sweden and in Finland and in our northern European SSSR. A number of Argentine wheat varieties which grow in their mother country in practically subtropical climate, with an absence of winter weather and a heavy annual rainfall up to and over 1000 mm., do well in our country, especially in the Leningrad section and the northern region. The barleys which we had collected in the mountains of Abyssinia, were found to perform excellently under the climatic conditions of Leningrad, notwithstanding the long summer days as contrasted with the short days of Abyssinia. The Abyssinian varieties of peas without special selection were also found to perform excellently under Leningrad conditions. On the other hand, the Abys-

sinian spring wheats from the same localities performed poorly in the Leningrad section and in all sections of European SSSR.

The blue and the yellow alfalfas of southern origin withstand the winters beyond the Arctic Circle and east of Finland. According to experiments of ZHEREBINA, the awnless varieties of brome grass collected near Voronezh withstand the winter without freezing in the extreme north.

To be sure there exists no perfect climatic and soil analogy. From the standpoint of plant introduction, the meteorological factors such as moisture and humidity are usually taken into consideration; but aside from these factors, there is the relative day length which changes with the latitude and is of great importance in plant introduction. The physiological experiments of ALLARD and GARNER and other investigators and also our own geographic experiments proved the great importance of photoperiodism in plant growth. The beets and turnips of southwest Asia, when transplanted into our northern regions change from biennials into annual plants. The Afghanistan radish has changed in the north from an oil plant with a thickened taproot into an annual plant without a thickened taproot (experiments of E. N. SINSKAYA).

As shown by direct experiments, great care is needed in applying the theory of climatic analogy in plant introduction. To the above listed examples can be added the observations on the Peruvian and Bolivian potatoes. Contrary to our expectations certain species and varieties of potato from these equatorial countries perform excellently beyond the Arctic Circle, where they not only bear tubers but also seed balls.

Also contrary to expectations, the formation of tubers and seeds in a number of South American potato varieties is especially pronounced in the extreme North.

The commonly employed method of equating zones of altitude with zones of latitude should be used with considerable caution, because this does not consider differences in photoperiodism.

However, in using climatic and soil data in breeding work, one should not overestimate the importance of climatic analogies. Thus, the statements of our very authoritative cotton breeder, G. S. ZAITZEV, that, on the basis of the climatic conditions for Central Asia, cotton would not do well in north Caucasus and southern Ukraine, proved to be incorrect. In the light sandy subsoils of north Caucasus and southern Ukraine and with a high seeding rate, the cotton plant shortens its phases of development and produces mature bolls, which was not understood from the data from Central Asia, where cotton is grown under irrigation and where the plants are widely spaced.

To speak with certainty of the suitability of a species or a variety to new conditions, it must be subjected to direct testing.

10. Quarantines in Plant Introduction:— The extensive development of plant introduction must go hand in hand with its regulation in order to prevent the introduction of new parasites. The organization of quarantine inspection is an essential part of plant introduction. Every parcel of seed from abroad should be examined by entomologists and phytopathologists. Infected plants should be fumigated and treated with fungicides and insecticides. In case of doubt the material should be sent to quarantine seeds plots for investigation. Special quarantine greenhouses are essential.

For this reason the importation of plants should be centralized and strictly controlled.

11. Introduction and Breeding of New Plant Varieties:— While in the breeding of cereals use is made of the original materials developed during thousands of years both in the Old World and the New, in the breeding of other crops (including fruits and berries) selections are made from the natural resources of the world's flora.

Hunger and the constant search for food have forced primitive peoples to select for their food all plants suitable for cultivation in temperate and subtropical climates. Great accomplishments have been made in this direction throughout past centuries by unknown breeders. One can only marvel at the diversity of varieties and species of wheat, barley, corn, sorghum, and legumes, all of which were known in primitive civilizations. It is not easy to find competitors to our present cereals; it would be very difficult to replace wheat, rice and corn by other cultivated plants. At any rate, world-wide botanical investigations, which had this for their aim during the last five decades, have resulted in the discovery of no new major crops. It is possible to change the existing varieties of wheat; it is also possible to create new species by crossing, and there is a great field open in this direction. However, the search for new genera of cultivated cereals is not promising.

Nevertheless, it is possible to create entirely new plants out of old forms, as, for example, the alkaloid-free lupines developed in recent years.

We have seen that an unlimited field for experiment is open in this direction in work with forage plants, among which there are hundreds of species deserving further breeding tests. This is true not only of plants utilized for grazing and for hay but also of those grown for the grain. Recent works of experiment stations in Italy and Portugal have shown that there is still much to be accomplished in the breeding of legumes grown for their seed. The Russian Institute of Plant Industry has succeeded in discovering a lupine containing 21% fat and 30% of protein, *i.e.*, a lupine which equals the soy bean in food value and at the same time is adapted to light soils.

There are many more possibilities for introduction of wild plants into cultivation for commercial use. In this field the plant breeders of former civilizations have accomplished relatively little. There is much to be done even in breeding fiber plants which have served as sources of raw material for many centuries. A new fiber plant is the Indian hemp which has been recently introduced into cultivation. It is interesting to note that in introducing this plant into cultivation, great difficulties had to be overcome in finding suitable eco-geographic forms.

An almost untouched field for experimentation is found among medicinal and ethereal oil producing plants.

Great possibilities exist in the introduction of new rubber plants suitable for cultivation in temperate and subtropical zones. Excellent examples are the new rubber plants, Tau-saghyz, Kok-saghyz, and Krym-saghyz, as well as the goldenrod of EDISON.

The cultivation of these plants again brought up the question of variety because investigations had shown that the different strains of Tau-saghyz and goldenrod greatly differed in the amount of rubber produced. *The question of new crops is invariably tied up with the finding of suitable varieties.*

The field of pigment plants and paper pulp plants is still untouched.

Among the wild fruit trees we find extremely interesting varieties of the almond, walnut and others which are in no way inferior to the best modern cultivated varieties. We find such varieties in the mountainous regions of Central Asia and Transcaucasia, not to mention the untouched resources of eastern Asia, which has literally hundreds of species of wild fruit trees.

12. **Vernalization and Its Significance in the Utilization of the World's Plant Resources:**— The method of vernalization introduced by T. D. LYSENKO opened up great possibilities for the utilization of the world's assortment of herbaceous crops. All our own old and new varieties, as well as the entire assortment of the world, should henceforth be tested from the standpoint of vernalization because experiments of recent years have shown that vernalization may give astonishing results by literally transforming plant varieties, changing them from plants ordinarily unsuitable for a given region into high-quality productive forms. For example, winter barleys which can not be grown under Leningrad conditions, since spring sowings fail to head and winter sowings are winter-killed, when vernalized, not only head normally but in some of the varieties have given higher yields than the best northern selections of spring barleys.

Certain vernalized varieties of long-fiber flax have grown taller than the untreated plants.

We are undoubtedly standing on the threshold of a revision of the world's crop resources, including our entire assortment of selected and local varieties in the sense of their reaction to vernalization. The method of vernalization is a powerful factor in breeding many herbaceous plants, enabling us to grow in our northern climes many southern subtropical forms which would fail to develop normally without this treatment.

Experiments with vernalization in the Khibin country beyond the Arctic Circle and in Leningrad have demonstrated great possibilities in the utilization of the world's assortment of various cultivated plants. For the first time we were able to experiment with the entire collection of barley varieties of the world, including both winter and late spring varieties which under ordinary conditions could never have headed in the Leningrad region.

In selecting suitable parents for hybridization, the theory of LYSENKO on "stages" also opens up unusual possibilities in utilizing the plant assortment of the world.

Conclusion:— We have barely begun the systematic study of the world's plant resources and have discovered enormous untouched reserves, unknown to scientific breeders in the past. The tremendous potential source of species and varieties requires thorough investigation employing all the newest methods. The problem of the immediate future is a classification of the enormous diversity of the most important cultivated crops not only on the basis of their botanical and agronomic characters but also with the use of physiological, biochemical, and technological methods. We should endeavor to develop in the near future a biochemical and physiological systematization of cultivated plants. The enormous plant potentials discovered in the centers of primary origin of forms and species of cultivated plants should be subjected to investigation not only by the taxonomist but also by the physiologist, the biochemist, and the pathologist. In the field of genetics, which aims at new creations through the most rational combinations of parents, an immense field of the most fascinating and urgent work is opened up.

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The LAW

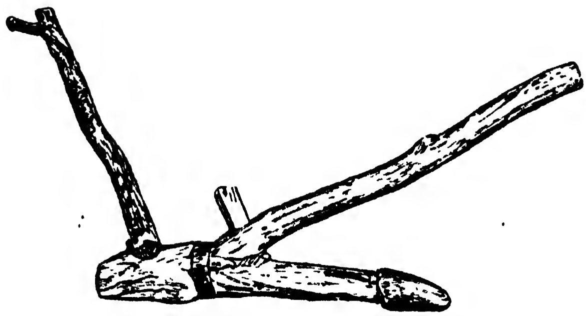
of

HOMOLOGOUS SERIES

In The INHERITANCE

of

VARIABILITY



Introduction[14]**:—** The characteristic feature of studies of the earth's vegetation, from TOURNEFORT to our own times, has been *the varied conception of systematic units.* Further investigations have done away with the general concept of species, introduced by LINNAEUS. The history of plant systematics, in particular that of cultivated plants, vividly illustrates the attempts to arrange, in a convenient and harmonious system, all the morphological and physiological characteristics, the number of which increases with finer methods for distinguishing heritable forms and the study of new specimens of the same plant, collected in different regions. Linnean species have become divided into subspecies and varieties, and varieties, in turn, into races. Genetic investigations of recent years, however, have proved the divisibility of even the most minute morpho-physiological units of systematics (elementary species in the sense of DE VRIES), and have shown that external uniformity may conceal distinct genotypes.

LOTSY, in his book "Evolution by Means of Hybridization" (1916) proposed a new terminology for distinguishing the basic units in the classification of hereditary forms. The old Linnean species, the heterogeneous character of which was brought out in the 19th Century, were not rejected, but considered as collective in nature, and these LOTSY distinguished as *Linneons,* in honor of LINNAEUS; races and varieties which make up the elementary species of JORDAN and DE VRIES, he proposed calling *Jordanons* in honor of JORDAN. The term *species* LOTSY reserved for genotypes, as basic units embracing genetically homogeneous groups of individuals. This last proposal, which is contrary to established botanical and zoological terminology, is inconvenient for practical usage, and, to avoid confusion, it is better not to use it.

Statistics of the Diversity of the Plant Kingdom:— The statistics of the plant kingdom deals for the present only with Linneons. HOOKER and ENGLER estimated the number of known species at 130,000 to 140,000 Linnean species of flowering plants including conifers. Present day botanists estimate the number of species of higher flowering plants at approximately 160,000. Richest in species are the families *Compositae* (about 14,000), *Leguminosae* (more than 13,000), and *Gramineae* (about 6,000).[15]

However large this number of Linneons may be, it gives little indication of the diversity of the earth's vegetation. A more concrete idea of the complexity of the plant kingdom is obtained only by a study of the Jordanons.

The systematic study of the numerous varieties within the limits of a Linnean species was begun by LINDLEY (monograph on roses), DE CANDOLLE (*Brassica*), KRAUS, METZGER, ALEFELD, and KÖRNICKE on cultivated plants and SÉRINGE, JORDAN, and NAEGELI on wild plants; in recent times these works on differentiation have been carried out by breeders and botanists (school of Swedish systematists: WITTROCK, DAHLSTEDT, ALMQUIST, and others).

The detailed study of plant races has revealed a lack of homogeneous, monotypic Linneons. Linnean species that were considered in the 19th Century as

[14] This is a translation, from the English, of our publication in the Journal of Genetics in 1922, with additions and changes. In Russian, "The Law of Homologous Series" was published in brief form in the Proceedings of the Third All-Russian Breeding Conference in Saratov.

[15] ENGLER: Syllabus der Pflanzenfamilien. 8. Auflage, 1919.

ultimate basic entities, in the 20th Century have been broken up by breeders and systematists into a great number of Jordanons, distinguished both morphologically and physiologically. As a classic example of the splitting up of a Linnean species we have *Draba verna,* the many heritable forms of which were considered as a unit in the 19th century, while in the 20th century the complex constitution of this species is regarded as a generally recognized established fact. Many cultivated and wild species of plants can be divided into a great number of well-distinguished heritable forms.

Thus, on the basis of the investigations carried out by us and our colleagues in the Institute of Plant Industry, wheat species are divided into a great number of forms that are readily distinguished, both morphologically and physiologically. Whereas ten years ago we determined the number of Jordanons of the soft wheat *Triticum vulgare* Vill., at approximately 3000,[16] at present, as a result of additional studies, this figure must be increased manyfold, and we cannot determine it even approximately. In this matter we are not dealing with artificial hybrids produced by breeders in the past 30 years, but principally with forms of wheat cultivated locally in the different regions of Asia and Europe. The diversity of wheat can be judged by the fact that there are distinguished today no less than 400 heritable morphological and physiological characters, which in most cases can freely combine in all directions, giving us the theoretical opportunity for millions of possible combinations.[17]

Thousands of Jordanons have been found in investigations of local Asiatic and African forms of barley. Even greater numbers have been found in oats. At the beginning of the 20th century the Italian botanist Comes found 700 botanical varieties in beans. Detailed investigations of recent years at the Institute of Plant Industry have increased the number of heritable forms of beans severalfold.

In rye—*Secale cereale*—which, not long ago was considered to be relatively uniform in comparison with wheat, there have been discovered hundreds of forms distinguished by morphological and physiological characters. They were found principally in the regions of Trans-Caucasus, Iran, and Afghanistan. The heritable forms of rice are numbered in the thousands. Varieties of corn are distinguished by hundreds of morphological and physiological characters. Also in the hundreds or thousands of varieties and heritable forms are divided peas, vetch, chickpeas, flax, lentils, beans, grasspeas, cotton, hemp, and sesame.

Detailed systematic investigations of important species of cucurbits carried out by K. I. Pangalo and his co-workers have disclosed a colossal diversity, with the determination of many thousands of forms. The same applies to fruits, vegetables, and potatoes.

In essentially every cultivated plant, whether it be tropical, subtropical, or a plant of the Temperate Zone, regardless of the family to which it belongs, with wide geographic differential study it becomes divided into a multitude of heritable forms, the number of which one can hardly estimate. We are obliged to limit the determination of differential heritable characters which can combine in many different ways.

Wild species vary no less than cultivated ones. This has been seen in the wild fruits of Central Asia and Caucasus which have been studied recently. Almost every wild plum tree in Trans-Caucasus shows some sort of heritable differences. It would be difficult to estimate the number of forms of wild apples and pears, quinces, pomegranates, and almonds. Scorzonera or Tau-

[16] N. Vavilov: [On soft wheat.] Trudi po Prikl. Bot. 13 (1). 1923.
[17] N. Vavilov: [Scientific Bases for Wheat Breeding.]

saghyz, the new source of rubber discovered on the shores of the Caribbean Sea, which is botanically no doubt one of the oldest plants, possibly from the Jurassic Age (M. V. KULTIASOV) shows literally thousands of well-distinguished forms. JORDAN and ROSEN discovered about 200 constant heritable forms in the wild *Draba verna.* The study of different wild plants of the Crucifer family (species of *Eruca, Brassica, Raphanus, Camelina,* and others) conducted by E. N. SINSKAYA has revealed a great number of forms. Hundreds of heritable forms have been found in the wild *Linnea borealis* (WITTROCK), *Picea excelsa* (WITTROCK), *Viola tricolor* (CLAUSEN), and others. Wild species of clover, sweet clover, yellow alfalfa, quackgrass, wild barley, foxtail grass, timothy, orchard grass, awnless darnel, wild oats, and many other forage grasses and legumes which have been studied in detail at breeding stations reveal no less variation in heritable characters than wheat, barley, oats, or peas. Monotypic species remain such only during the time when they are studied exclusively in the herbarium. When they are studied in culture with large numbers of specimens, inevitably the polymorphic nature of the species is revealed.

No less diverse are plants that are propagated today by vegetative or apogamous means, such as roses, potatoes, tree fruits, citrus fruits, and dahlias. One has the general impression that the more we study plants or animals, the more variable they appear to be, and the more varieties there are discovered within the limits of a Linnean species. Some Linnean species of plants, such as wheat, corn, rice, date palm, roses, apples, pears, pomegranates, peaches, apricots, cabbage, lettuce, and squash show an unusual amount of variability; the same applies to species of domestic animals and to *Drosophila* but this is evidently due to the fact that these have been investigated more than other species of animals.

The differences between Jordanons within the limits of a given Linneon, with respect to form and color of flowers and to form and dimensions of leaves and other organs, are no less striking than the differences between Linneons in many cases. For example, some forms of the squash, *Cucurbita pepo,* have fruit about the size of a hen's egg, while other members of the same species, growing under the same conditions, have fruits reaching a half meter and more in diameter. Varietal differences with respect to weight of fruit in the bottle gourd, pear, and apple within the limits of a single Linneon, are as great as a thousandfold; the same is true of root crops, for example, radish.

Varieties within the limits of a single species of sesame are distinguished from one another by important systematic characters which in other plants would serve to distinguish species, and even families, for example, opposite or alternate position of leaves and fruits, fused or separate valves of the fruits, position of the blossoms, whether single or in threes, and others. In some forms of wheat and rye the leaves lack a ligula, *i.e.,* they do not show the customary differentiation of the leaves into leaf sheaths and leaf blades.

On the other hand, such a common alternating character in varieties of the majority of plants as the presence or absence of anthocyanin in stems and shoots, appears to be specific throughout the entire family of cucurbits. Despite an extended search among thousands of varieties of watermelon, muskmelon, squash, and gourds, we have not once found forms with anthocyanin in the stems or shoots.

The similarity of polymorphism in both cross-pollinated and self-pollinated plants. The uniformity of some cross-pollinated plants is only apparent in cases where it has not been investigated. The only difference is that in cross-pollinated plants characters are often found in a heterozygous condition, while

in self-pollinated plants they are often homozygous. In cross-pollinated plants many recessive characters may not be recognized as a result of the dominance of other characters.

In deliberate self-pollination of these plants (Inzucht or inbreeding) there can be discovered a great diversity of recessive forms. Investigations of recent years on corn, sugar beets, rye, and sunflowers by self-pollinating the plant, have revealed a multitude of original recessive forms, still more increasing the variability known to exist in these plants. But even without deliberate inbreeding, many cross-fertilized plants such as corn, rye, and beets, and many domestic animals, even man himself, show no less variability than self-fertilized organisms.

* * * * *

There arises the urgent problem of the systematic study of Jordanons within the limits of species, particularly in cultivated plants and domesticated animals. This is indispensable to the purposes of genetics as well as agronomy. Only by means of detailed study of Jordanons and genotypes can we arrive at the correct understanding of species. In order to determine genetic formulas of variation it is necessary to know the constitution of the Linnean species. Before proceeding to the creation of new varieties by crossing, it is necessary to know the existing forms in nature.

In 1880 Alphonse de Candolle, in his remarkable book "La Phytographie" wrote:

> "There will come a day when science will treat the elements of species just as the elements of genera and families, and all these groups will be coordinated into a perfectly uniform system." (Page 80).

This day has arrived.

But the problem is not a simple one. A detailed study made by us on a number of cereals, legumes, cucurbits, composites, mallows, and flax has convinced us of the complexity of this undertaking. To give an exhaustive list of the variations of animals and plants, even of the principal groups, is an almost insuperable problem.

The near future promises an extension of the Linneons, and a multiplication of the number of Jordanons. Artificial hybridization and mutation, and the use of inbreeding and crossing threaten to produce, in the near future, a significant increase in the external variation in form, and already at the present time it is expedient to determine the extent of variation within the limits of Linneons, not by the number of described and possible combinations, but *the number of varietal characters which distinguish the different forms from one another.* In this connection we must not forget that various characters may be conditioned by several hereditary factors, *i.e.,* may have complex formulas of inheritance.

The numberless variations, the chaos of endless forms, compel the investigator to follow the route of systematization or synthesis. The process of differentiation of Linneons has been going on for a long time; it is inevitable and indispensable, for an enumeration of forms existing in nature, to have a correct presentation of the constitution of the plant world, and to have clearly in mind the route which must be followed in man's work in creating new forms. As the biological investigations go deeper they pass from morphological characters to physiological and biochemical properties. Ahead of us lies differential systematics based on biochemical and physiological differences within the limits of a species. But parallel with differentiation, naturally, it is necessary for us to *integrate* our knowledge of varieties, races, and Linneons themselves. If

160,000 Linneons are already the prodigious number with which the investigator must laboriously deal, even more complex will be the work with tens and hundreds of millions of Jordanons.

Next before the investigators of the animal and plant world there arises the urgent problem of explaining the regularities in intraspecific polymorphism and of classifying the phenomena of polymorphism, a similar problem to that which in its time existed in the study of the world of inorganic and organic chemicals.

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In studying in detail the race constitution of world vegetation, one can note certain regularities in the diversity in the varieties and races which are contained within Linnean species, despite their great polymorphism.

An attempt has been made to integrate the phenomena of intraspecific polymorphism and present the underlying regularity which we have observed in studying the forms of the plant kingdom, and which we have called "the Law of Homologous Series in Heritable Variation" (1920).

The Concept of Parallel Variation:— The basic idea of uniformity in the inheritance of organic matter was developed philosophically in its basic features by GOETHE in his "Metamorphosis of Plants" and also in the idea of uniformity in diversity developed by GEOFFROY ST. HILAIRE (1828) and DRESSER.[18] This idea, particularly after DARWIN and under his influence, penetrated comparative anatomy and morphology of animals and plants.

Isolated facts of parallel heritable variation in closely and distantly related species have been known for a long time. The botanist, NAUDIN, noted them clearly in his classic investigations of cucurbits in the middle of the 19th century. DARWIN, in the breadth of his grasp of the problems of evolution and his careful study of variations, could not by-pass the fact of parallel variation which, he considered, occasionally occurs in plants and animals.[19]

In "The Origin of Species," in the chapter on Compensation and Economy in Growth, DARWIN emphasizes that "various species show analogous changes in such a way that one species acquires the characters of other related species or reverts to characters of an earlier ancestor."

At the beginning of the section on analogies or parallels in variations (Variations of Animals and Plants under Domestication) DARWIN writes:

> "By this term I mean that similar characters occasionally make their appearance in the several varieties or races descended from the same species, and more rarely in the offspring of widely distinct species. . . . The cases of analogous variation, as far as their origin is concerned, may be grouped, disregarding minor subdivisions, under two main heads; firstly, those due to unknown causes acting on similarly constituted organisms, and which consequently have varied in a similar manner; and secondly, those due to the reappearance of characters which were possessed by a more or less remote progenitor."

In this, DARWIN is alluding to the facts reported by NAUDIN for cucurbits

[18] GEOFFROY ST. HILAIRE: Sur le principe de l'unité de composition organique, Paris, 1828.

CHRISTOPHER DRESSER: Unity in variety, London, 1860.

In recent years there have been published a number of works devoted to the unity of the phenomena of life. *Cf.* K. MARBE: Die Gleichförmigkeit in der Welt. Bd. I und II. München, 1916-1919. P. KAMMERER: Das Gesetz der Serie. 1919.

[19] DARWIN: Variation of Animals and Plants. Part 2, Chap. XXVI "Analogous or Parallel Variation." London, V. Murray, Popular edition in two volumes, 1905.

and to the entomologist, WALSH's Law of Equable Variability (1863),[20] which runs as follows:

> "If any character is variable in one species in a given group there will appear a tendency to variation also in other related species; and if any character is entirely constant in one species of a given group, it will tend to be constant in related species."

In the entire evolutionary conception of DARWIN, however, this law of the variation of species receives no further development.[21] WALSH, himself, in a special publication on the systematics of the *Neuroptera* gives a short formulation of the Law of Equable Variability and a few examples of its application in entomology but does not develop this generalization further.

The French botanist M. J. DUVAL-JOUVE collected a large number of facts on variation of wild species of grasses, rushes, and sedges in his "Variations parallèles des types congénères" published in 1865 in the "Bulletin de la Société Botanique de France," Volume 12. Its conclusions are in good agreement with our law. HUGO DE VRIES in his "Mutation Theory" and "Pangenesis" also notes a series of parallel variations. EIMER in his study of orthogenesis supports the same theme, but from another point of view.[22]

A number of paleontologists such as COPE and OSBORN have noted trends toward parallel variations in animals. Recently SACCARDO and ZEDERBAUER have given striking examples of parallelism in fungi and conifers. The entire system of fungi in the monumental classic work of SACCARDO is based on the law of analogous variation.[23]

Fragmentary indications from systematics, on the regularity and parallelism in variation in different groups of plants and animals and particularly insects, show the wide distribution of this phenomenon.

Detailed studies of the variations within many species, and a great quantity of new facts, collected principally on cultivated plants and those wild plants that are most closely related to them, permit us now to approach this problem anew and to bring together all known facts in the form of a general law to which all organisms conform, and which, it is our conviction, must have a basic place in systematizing our knowledge of the inheritance of the variations in species.

1. **Variation in Related Linneons:**— In studying the racial composition of the world vegetation in certain related Linnean species within the limits of single genera, despite a sharp expression of polymorphism of many species, one can note a number of regularities in the diversity of the varieties.

The first regularity seen is a similarity in the morphological and physiological characters which distinguish different varieties and races (Jordanons), constituting related Linneons. A detailed study of species in extensive materials collected in different geographic areas, shows a parallelism in phenotypic variation in Linnean species within the limits of a given genus.

We will take up a few concrete examples.

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[20] Proc. of the Entomolog. Soc. of Philadelphia. Oct. 1836. P. 213.

[21] Only in the quotation from DARWIN in "Variation of Animals and Plants in Domestication" is the Law of Equable Variability given wider application in the field of biology.

[22] G. H. T. EIMER. Die Entstehung der Arten auf Grund von erworbener Eigenschaften nach den Gesetzen organischen Wachsens. Vols. I-III, 1888-1901. Jena.

[23] P. A. SACCARDO. "I Prevedebilli Funghi Futuri secondo la Legge d'Analogia." Degli Atti del R. Istituto Veneti de Scienze, Lettere ed Arti, Tomo VIII, Ser. 7, 1896.

E. ZEDERBAUER. "Variationsrichtungen der Nadelhölzer." Sitzungsberichte d. Akademie d. Wissenschaften, Wien, Nat.-Math. Klasse, 116, Abt. I, 1907.

Wheat.—We are considering the species of cultivated wheat. As shown by numerous investigations, the species of wheat are grouped into the following three genetic and geographic types, distinguished according to their numbers of chromosomes (2x = 14, 28, 42).

GROUP I (42 chromosomes): (Basic area: S. W. Asia)	*Triticum vulgare* Vill. *Triticum compactum* Host. *Triticum spelta* L. *Triticum sphaerococcum* Perc. *Triticum macha* Decap. *Triticum vavilovianum* Jackub.
GROUP II (28 chromosomes): (Basic area: Abyssinia, Trans-Caucasus, and the Mediterranean region)	*Triticum durum* Desf. *Triticum turgidum* L. *Triticum polonicum* L. *Triticum dicoccum* Schr. *Triticum persicum* Vav. *Triticum timopheevi* Zhuk.
GROUP III (14 chromosomes): (Basic area: Asia Minor and Trans-Caucasus)	*Triticum monococcum* L.

Triticum vulgare—soft wheats, with many varieties and races divided into the following groups: *1*) awned, awnless, and semi-awned forms with bent awns and inflated glumes (*inflatum*); *2*) white-, red-, grey-, and black-headed forms; *3*) forms with hairy glumes, with smooth glumes; *4*) forms with white or red grains; *5*) winter and spring types, etc.

The species which are closely related to soft wheats, *T. compactum, T. spelta, T. sphaerococcum,* and *T. macha,* exactly duplicate the variations of soft wheats that have been given.

We pass to the second genetic group of wheats characterized by 28 chromosomes. In general they repeat the series of characters found in the first group. Here, too, we find forms with white, red, or black heads, forms with glumes that are smooth or hairy, with white or red grains, and of winter or spring types. Here also are found forms that are awned, short-awned, awnless, and inflated types. (See FIG. 2).

The third group, the 14-chromosome wheats, includes the species *T. monococcum* which duplicates the second group in its varietal constitution. Here we only fail to find awnless forms, but we do find varieties with long and short awns, as well as forms with white, red, or black heads, with smooth or hairy glumes, and with red or white grains.

The wild form of wheat, *T. dicoccoides* Körn. which is characterized by 28 chromosomes and today is found in considerable quantity in Syria, northern Palestine, Armenia, and near Nakhichevan, and the wild single-grained wheat, *T. aegilopoides* (with 14 chromosomes) each consists of a large number of varieties basically similar to those in the other species of cultivated wheat, mentioned above.

Numerous races within the limits of different botanical varieties of a given species of wheat reveal an even greater similarity in detail.

Barley.—Cultivated barley contains two species or subspecies that are very closely related genetically and are easily crossed with each other: *Hordeum vulgare* and *H. distichum.* The first of these contains the following forms:

1. Compact-headed, loose-headed
2. Yellow-, red- (with anthocyanin), and black-headed
3. With smooth or hairy glumes
4. With hull-less or hulled grain
5. Awned, short-awned, awnless, and furcate (type *trifurcatum*)
6. With smooth awns or with barbed awns
7. Winter or spring type

Both species of barley duplicate the same series of characters.

Until quite recently there was known only one variety of wild barley (*Hordeum spontaneum* C. Koch), closely related to *H. distichum* L. This form was of winter type and characterized by yellow heads. In our investigation in Iran, Turkoman, and Afghanistan, there were found a number of new forms of wild barley, among which were varieties with black or brown heads, and with smooth or hairy glumes. Among the winter types were found typical spring varieties. Parallel forms with colored heads were found also in the wild species, *Hordeum murinum.*

Oats.—Here we are considering oats of the section *Euavena,* including the cultivated species and the most closely related wild oat species. Study of a large number of forms at the Institute of Plant Industry (A. I. Maltsev, N. I. Vavilov, and A. I. Mordvinkina) has shown that the species *A. diffusa* Asch. & Gr., *A. orientalis* Schr., *A. fatua* L., *A. ludoviciana* Dur., *A. sterilis* L., *A. byzantina* C. Koch., *A. brevis* Roth., *A. strigosa* Schreb., and *A. barbata* Brot., as well as *A. abyssinica* are all characterized by similar series of varieties with white, yellow, grey, or brown glumes that are either smooth or hairy. In many of these species there were found both spring and winter forms and forms that were either early or late.

Millet.—The same parallelism can be found in a study of related species within the genus of millet. *Panicum italicum, P. miliaceum,* and *P. frumentaceum* present a striking example of species which are sharply distinct and which at the same time show a common diversity of botanical varieties. In compactness of the panicle, in the color of the glumes, in the presence or absence of awns, and in the development of anthocyanin pigment in the heads, these species repeat one another. The differences go deeper. Among the forms of both *Panicum italicum* and *P. frumentaceum* are found races which are distinguished by the reaction of the endosperm to iodine in potassium iodide. One of these forms colors red, the other blue, which indicates differences in the chemical composition of the endosperm.

Cotton.—Comparing Asiatic cotton, *Gossypium herbaceum* L., which is widely cultivated in Iran, Afghanistan, and Kashgania (China) with the Indian cotton *G. arboreum* L. and also with American species *G. hirsutum* L., Upland cotton, and *G. barbadense* L., the so-called Egyptian cotton, one cannot fail to note a striking similarity in the series of variations even though these species are separated by continents, as has been brought out in the investigations of G. S. Zaitsev, S. E. Harland, and F. M. Mayer, and other authors. Varieties of these species resemble one another with respect to variation in fiber color (white, brown, green) presence or absence of hairiness, color of the seed, type of branching of the entire plant (monopodial, sympodial), form of leaves, color of stems, and presence of forms with open or with closed bolls. This is in spite of the fact that the American and Asiatic cottons are sharply distinct with respect to numbers of chromosomes (52 and 26) and to difficulty in crossing them with each other.

Agropyrum repens and *A. cristatum.*—In comparing the polymorphism of the Linnean species *A. cristatum* and *A. repens,* crested wheat grass and quackgrass, two species which are widely distributed in European and Asiatic parts of SSSR, and which have been intensively studied by V. S. Bogdano and P. N. Konstantinov, one cannot help noting the striking resemblance in the series of variations in these two independent species. Both of them have:

1. Awned and awnless forms
2. Hairy and smooth-glumed forms
3. Yellow, red (with anthocyanin), and black-headed forms

4. Forms with recumbent, erect, and intermediate habits
5. Forms with thin straw and others with thick straw
6. Narrow-leaved and wide-leaved forms
7. Compact-headed and loose-headed forms
8. Forms with and without a waxy coating
9. Forms with yellow and others with violet anthers
10. Low-growing and tall-growing forms
11. Forms with hairy and others with smooth leaves
12. Late and early forms
13. Hydrophilic and xerophilic types

In crested wheatgrass there are forms with solid straw, while such are unknown in quackgrass, but quackgrass has been studied too little to permit one to conclude as to the presence or absence of such forms. The investigations of the Canadian botanist MALTE (1932)[24] definitely show that in other species of *Agropyrum* in North America there appear the same homologous series of forms.

Brassica napus and *B. rapa.*—A clear-cut parallelism of the series of forms is observed also in *B. napus* and *B. rapa.* In both there are annual and biennial varieties when these are cultivated under uniform conditions. With respect to color and form of the blossoms and leaves, to the habit of the plant, and to the color and form of the roots, there are observed parallel series in both Linneons (See E. N. SINSKAYA, "Oil and Root Crops of the Family *Crucifereae*," Trudi po Prikl. Bot., Vol. 19, Part 3, 1928).

Cucumbers and cantaloupes; different species of cucurbits.—A striking parallelism of varieties can be traced in cucumbers and cantaloupes, belonging to two different Linnean species *Cucumis sativus* and *C. melo,* which are quite distinct physiologically as has been shown by NAUDIN. In form of fruit, color, seeds, and leaves, in details of the structure of the blossoms, and in general appearance of the plant, it is impossible to overlook the marked resemblance of the variations of these two Linneons, which contain large numbers of well-distinguished Jordanons. Some of the cantaloupes are strikingly reminiscent of forms of cucumbers in external appearance, and even in flavor.

The same series of parallelism of Jordanons can be observed in other cucurbits, as, for example, in *Cucurbita maxima, C. pepo,* and *C. moschata* (*Cf.* Trudi po Prikl. Bot., Vol. 23, Part 3, 1929/30, on cucurbits, edited by K. I. PANGALO).

A large number of similar facts and examples could be introduced from different cultivated and wild plants.

Such parallelism in variation does not appear to be fortuitous, but entirely general. Whereas in the time of DARWIN such facts were isolated and disconnected, today as a result of detailed study of a great number of Linneons found in different families and involving investigations of new materials, there is no doubt of the generality of this law.

A priori, one might think that series of parallel variations would not always necessarily be complete in all species which have been submitted to the effects of natural selection during hundreds or thousands of years; this is all the more probable since some of the combinations of genes appear to be lethal. In the historical processes of development, some species have become extinct, as is demonstrated by the findings of paleontology. It is therefore not surprising to find a lack of certain connecting links in series of existing forms within the limits of Linnean species.

An exhaustive botanical study of a great number of cultivated plants and

[24] MALTE, M. O. The so-called *Agropyrum caninum* (L.) Beauv. of North America. Annual Report (1930). National Museum of Canada, Ottawa, 1932.

their wild relatives, based upon the extensive collection of world materials gathered by expeditions of the Institute of Plant Industry, has revealed a complete series of heritable forms within the limits of many species, surpassing our expectations. This study has shown the existence of a striking parallelism in variation, examples of which have been given; others will be given later.

Thus we come to the conclusion that genetically close Linnean species are characterized by resemblances in their series of heritable forms, and it is observed that the closer species are related genetically, the more exact is the repetition of series of morphological and physiological characters. *Linneons that are closely related genetically are characterized, consequently, by uniform series of heritable intraspecific variations.*

2. **Variations in Different Genera:**— *Rye and Wheat.*— In comparing the racial constitution in related genera, we can observe the same regularity in polymorphism. We will compare wheat and rye.

Until quite recently rye (*Secale cereale*), despite its wide distribution in culture, has been little studied with regard to varietal constitution, since varieties of rye, being cross-pollinated, are not sharply distinct, and the division of the species into heritable forms is more difficult than in wheat. Our investigations with our colleagues A. Yu. Freiman-Tupikova and V. F. Antropova on specimens of rye collected from different localities in Iran, Trans-Caucasus, Afghanistan, Uzbekistan, and Tadzhikistan, have revealed the presence of a distinct polymorphism in rye, no less than in wheat, and, which is particularly interesting, the group of characters distinguishing the forms of rye when they have been fully exposed, show in detail races and varieties comparable to those in wheat. For example there were found in rye as well as in wheat forms with the following contrasting characters:

1. Awned, half-awned, and almost awnless forms
2. Forms with hairy, and others with smooth heads
3. Forms having red, white, black, and violet heads
4. Green (typical), white, red, brown, and violet-grained forms (Green forms are also found in wheat. Violet-grained wheats are found in Abyssinia.)
5. As in wheat, forms with grain that is easily, or only with difficulty, separated from the chaff
6. Forms with solid, and others with hollow straw
7. Forms with brittle, and others with tough rachises
8. Winter and spring grown types
9. Compact and loose-headed forms
10. Forms with and without a waxy coating on the heads
11. Forms with simple, and others with branched heads
12. Long- and short-headed forms.
13. Forms with hairy, and others with almost smooth rachises
14. Forms with wide, and others with narrow glumes
15. Forms with and without awnlets
16. Forms with hairy, and others with smooth leaf sheaths
17. Forms with violet, and others with green seedlings
18. Forms with a large number of blossoms in a spikelet, and others with only two blossoms
19. Forms with coarse, and others with delicate awns
20. Forms with grain that is vitreous, and others with mealy grain
21. Forms with large, and others with small grains
22. Forms with wide, and others with narrow leaves
23. Forms with smooth, and others with hairy leaves
24. Forms with, and others lacking a ligula (*eligulatum*)
25. Forms with long, and others with short straw
26. Forms with dense, erect growth, and others with a falling habit
27. Late and early forms
28. Forms that are self-pollinated, and others that are cross-pollinated

In a word, the genus *Secale* in detail repeats the genus *Triticum* in its species composition—a fact which was entirely unsuspected when the investigation began. The experiment was so carried out that we discovered in rye those same characters which were known in wheat, and our presumption of the existence of this or that form on the basis of the Law of Homologous Series in Variation was usually verified by investigations of new geographical materials from sources in the native home of rye. For example, in 1917 we found in specimens of soft wheat from Palmyra (in Shugnan and Afghanistan) several varieties with simplified leaves, lacking ligulae and auriculae. Such forms up to this time had not been known in the botanical literature. *A priori,* on the basis of the parallelism of polymorphic series, we foresaw the possibility of the existence in nature of forms of rye without ligulae. In 1918 we were able to confirm our supposition: such forms were found in a detailed study of spring rye varieties from Palmyra (FIG. 4).

In the literature there had not been reported forms of cultivated rye with hairy glumes. *A priori,* the existence of such forms was very probable, since in the related genus of wheat, all the Linneons contained forms with smooth glumes and others with hairy glumes. In 1918 hairy forms of rye were found among specimens from Palmyra and later in specimens from Armenia.

In rye, just as in wheat, were found forms with long awns, semi-awned forms, and forms that were almost awnless.

The parallelism of the series of variations in rye and wheat is understandable from the evolutionary point of view, since these genera are quite closely related to one another genetically.

Wheat and rye naturally hybridize. It is most striking to find here a complete parallelism in variation in the last detail.

Aegilops and Agropyrum.—The genus *Aegilops* which is closely related to *Triticum* and which grows extensively in a wild condition in SSSR, Asia Minor, Iran, northern Afghanistan, Central Asia, and the region along the shores of the Mediterranean Sea, on the whole repeats the diversity characteristic of the genus *Triticum.* In the species *Aegilops squarrosa, A. crassa,* and *A. cylindrica* as well as in *A. ovata* and *A. triaristata,* we now know that there are awned as well as awnless forms, varieties with yellow, red, and black heads, and with smooth and hairy glumes. There are known to be both winter and spring varieties in Linneons of this genus. Furthermore, the division of the genus *Aegilops* itself into Linneons to marked degree runs parallel with that of the genus *Eutriticum.* *A. squarrosa, A. crassa,* and *A. cylindrica* are most closely related to *Triticum vulgare* or to Linneons of the same group of wheat. These species are characterized by hollow straw and susceptibility to stripe and leaf rusts (*Puccinia glumarum* and *P. triticina*), to powdery mildew (*Erysiphe graminis*), and to smuts, just as are the soft wheats. Other Linneons such as *Aegilops triuncialis* and *A. ovata,* which correspond more to *T. durum* or *T. monococcum,* are immune from the enumerated parasitic fungi, and are characterized by solid straw as in the hard wheats.

The genus *Aegilops* is also quite closely related to *Triticum* as is shown by the possibility of obtaining hybrids between members of the two genera.

The genus *Agropyrum,* although systematically somewhat more distantly related to wheat than rye or *Aegilops,* nevertheless does have some degree of relationship since some of its species hybridize with wheat.

In 1919 we obtained sterile hybrids (F_1) by crossing *Secale fragile* with *Agropyrum villosum.*

CHERMAK obtained fertile amphidiploids by crossing wheat with *Agropyrum villosum.* Recently N. V. TSITSIN and other investigators have obtained

fertile hybrids between certain species of quackgrass and wheat. As we have already seen in the examples of *A. cristatum, A. repens,* and others, these species repeat the variations of characters found in the genera *Triticum* and *Secale.*

Vicieae.—We turn to the family of legumes. Four Linneons—*Pisum sativum, Lathyrus sativus, Lens esculenta,* and *Vicia sativa*—belong systematically to the section *Vicieae.* Their botanical composition has been studied in detail at the Institute of Plant Industry, the study being based on extensive materials collected in different European and Asiatic regions (about 8,000 specimens). All four species show similar homologous series of variations. All of these Linneons vary similarly with respect to colors of blossom and seed. Along with white-flowered forms, there are varieties with anthocyanin, rose-colored, purple, blue, forms with yellow petals (flavone pigment), and forms with spotted or striped blossoms. There are forms with small and others with large leaves, and forms with or without a waxy coating on the leaves and stems. All four genera show uniform variability in color of the cotyledons (green-yellow versus orange-red). In all four genera there are heritable forms from white-seeded to black-seeded, including yellow and green-seeded ones. Along with uniformly colored seed, in all genera there are found races with spotted and marbled seed, with small and large seeds, forms with white and black scars, flat, angular, and spherical seeds, and forms with smooth and wrinkled seed surfaces. Also in the four genera there are forms that are low-growing or dwarfed as well as normal ones, and early and late forms. In all four genera there are found forms with narrow and wide leaves and with leaves covered with wax or lacking this feature, and with stems and leaves containing anthocyanin or lacking it. Variations in the fruits of all species proceed in the same direction.

The resemblances in species of the *Vicieae* are so striking that frequently it is difficult to tell from the external appearance of the seeds to which genus a given sample belongs (FIGURE 3).

Cucurbitaceae and Other Families.—The principal cultivated species and genera of the family *Cucurbitaceae* are: watermelons—*Citrullus vulgaris;* cantaloupe—*Cucumis melo;* cucumber—*Cucumis sativus;* and the squashes—*Cucurbita pepo, C. maxima,* and *C. moschata.*

According to the investigations of NAUDIN all three genera belong to two related sections, the *Cucumerinae* and the *Cucurbitinae,* and thus we can compare their variability. A great number of varieties collected in different regions were investigated, beginning in 1919, at first by us personally and our co-workers, and later by K. I. PANGALO. The most thoroughly studied species of all three genera are characterized by varieties with round, oblong, flat, and simple or segmented fruits. The variations in color of the fruits are quite similar in all genera: they are either uniformly colored, striped, or spotted, and white, green, yellow, brown, or black. The parenchyma of the fruits is either colorless or contains colored plastids. With respect to taste they are divided into sweet and bitter forms. Variations in the size of the fruits are very great in all of these genera: from small fruits no larger than a hen's egg to giant fruits such as our common squashes, cantaloupes, or watermelons. Differences in the structure of the flowers in color and hairiness of the corolla and calyx vary in the different forms, and in general these differences are similar in all genera. The leaves also vary in all three genera. The majority of varieties of cantaloupe are characterized by simple leaves quite distinct from the deeply-lobed leaves of the ordinary watermelon, but we found forms of cantaloupe with lobed leaves, as in typical watermelon. On the other hand we found watermelons with simple leaves, characteristic of cantaloupes.

Varieties of *Cucurbita pepo* have leaves ranging in form from those as in cantaloupes to those as in watermelon.

Along with the usual creeping forms of cantaloupe, in Afghanistan we found bushy types reminiscent of the habit of growth of pumpkins.

Cases have been found among squashes where it has been difficult to determine, from the external appearance of the fruit, or even after cutting it open, to which genus it belonged. The similarity in variation of different characters is so marked in the *Cucurbitaceae* that even careful botanists, such as the late S. I. KORZHINSKI, have reported non-existent natural hybrids between cantaloupe and watermelon,[25] on the basis of the characters involved.

In the agricultural literature one can find reports of fertile hybrids between cantaloupes and squashes. Careful experiments carried out by NAUDIN and other workers and also at the Institute of Plant Industry, have given negative results. Even different Linneons within a single genus, such as *Cucurbita moschata, C. maxima,* and *C. pepo,* can be crossed with one another only with great difficulty. Despite many attempts, we have never yet been able to cross watermelon with cantaloupe or watermelon with squash and obtain fertile hybrids.

The intermediate forms found in nature and erroneously considered to be natural hybrids between these genera because of leaf form, seed structure, and taste, are excellent illustrations of the resemblances in variation among these genera. This is the case with the variations in the so-called "hybrids" between watermelon and cantaloupe described in detail by KORZHINSKI.[26] Analogous forms are known to exist among the grains.

For us the important fact is that despite the extraordinary variability among these genera and species, the variations show definite regularity. Knowing the series of variations in watermelon varieties, we can search for the same series of forms in cantaloupes and squashes.

A regularity of variability has been observed in striking form in the family *Cruciferae* in different genera—*Brassica, Eruca, Sinapis, Raphanus, Lepidium, Cardamine,* and *Capsella*—with respect to the form of leaves. arrangement of blossoms, hairiness of fruits and shoots, color of seed, color of blossoms, and division into winter and spring forms, as well as other characters. The more specimens we examine and the more carefully we study the content of heritable forms within the limits of a species, the more clearly appears this parallelism.[27]

Closely related genera in the family *Solanaceae,* such as *Capsicum, Lycopersicon,* and *Solanum,* also are striking examples of parallel variability. The family *Pomaceae,* in numerous species of Eurasian origin, clearly demonstrates the regularity in variation. A comparison of the species of pears of Eastern Asia, Caucasus, and Central Asia, and their varietal constitution, with species of apples, quince, and other genera, clearly brings out their resemblance in variation of fruit, blossom, leaf, and stem characters. The same thing may be observed in species of the genus *Prunus:* apricots, prunes, plums, and cherries.

The phenomenon of homologous variability in related genera can be traced in the most diverse botanical families, including monocotyledons, dicotyledons, and even conifers (ZEDERBAUER).

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[25] S. I. KORZHINSKI. "Bastarde zwischen *Citrullus vulgaris* und *Cucumis Melo.*" Bulletin de l'Académie des Sciences de St. Pétersbourg. 1897.

[26] N. I. VAVILOV. "On intermediate hybrids of cantaloupe, watermelon, and squash." Trudi po Prikl. Bot. 14, Pt. 2, 1925.

[27] E. N. SINSKAYA. "On regularity in variability in the family *Cruciferae.*" Trudi po Prikl. Bot. 13, Pt. 2, 1923.

Despite the important role of natural selection and the dying out of many connecting links, as the facts show, it is not difficult to demonstrate the resemblance of inherited variations in closely related genera.

Thus, *the second rule or law in polymorphism,* resulting from the nature of the first, *is that not only closely related species, but also genera show similarities in the series of inherited variations.*

3. **Variability in Whole Systematic Families:**— The study of a large number of genera within the limits of a family makes it possible to find general tendencies in variability that apply to all genera of the family.

Gramineae.—We will examine the most thoroughly studied family, *Gramineae,* and consider first of all the basic divisions of the several genera and species into varieties. All cereals and grasses may be divided according to *structure of inflorescence.* Millet, as is well known includes ramose, more compact, drooping, and ball-like types of inflorescence. The same divisions occur in sorghums. Oats are divided into forms with compact inflorescences with short internodes and branches, and ramose types which are subdivided according to the degree of looseness of the panicle (Schlafrispe, Steifrispe). The division of oats is essentially similar to that in varieties of millet and sorghums. The same divisions occur in different species of millet, such as *Panicum italicum* and *P. frumentaceum.* Cereals are divided into loose-headed, compact-headed, and intermediate types. In rye, wheat, and barley, we have a clear expression of divisions according to compactness of the inflorescence. Varieties of corn are also divided according to the compactness of the cob. Varieties of rice may be separated in a similar fashion, according to compactness of the inflorescence. The pasture grasses which have been investigated from this point of view, such as *Festuca pratensis, Phleum pratense, Bromus inermis, Dactylis glomerata, Agropyrum repens,* and others, all may be subdivided according to looseness or compactness of the inflorescence.

Throughout the entire family of *Gramineae* the varieties may be divided into awned and awnless forms.

The type of articulation of spikelets found in the closely related wild relative of cultivated barley, *Hordeum spontaneum,* characterized by easy breaking off or shattering when ripe, or an analogous type of shattering which occurs in the wild species of the cultivated oat, *Avena fatua* and *Avena ludoviciana,* with scars at the base of the spikelet—is found in many genera and may be demonstrated in *Secale, Triticum, Agropyrum, Oryza, Andropogon, Alopecurus, Phleum,* and others. It also appears in the wild genus related to corn, *Teosinte,* and in all species of cultivated millet and their wild relatives.

A branched inflorescence, as a racial variation, is characteristic not only of many species of wheat and rye, but also a large number of other genera that normally have head-like inflorescences. It has been found in species of *Agropyrum, Lolium, Hordeum,* etc.

The whole family of grains and grasses can be divided into hulled and hull-less forms, *i.e.,* into forms with grain which is tightly enclosed by the glumes and others in which the grain easily separates from the glumes. Such forms are known in wheat, barley, rye, corn, millet, sorghum, and foxtail.

According to color of the mature glumes the grains and grasses may be divided into types with five basic colors: white, yellow, red, gray, and black or dark brown. Such forms have been found in wheat, barley, rye, oats, rice, millet, sorghum, *Aegilops, Agropyrum,* foxtail, and other genera.

Nilsson-Ehle found among cultivated oats a variety lacking a ligula (form *eligulatum*). We have also obtained such forms in wheat and rye.

Emerson and Collins in America have observed similar forms in corn, and D. E. Yanishevski has also discovered such forms in *Poa bulbosa*. A. N. Lutkov (1935) has obtained eligulate mutations in barley.

Almost all Linneons belonging to the most diverse genera of cereals and grasses can be divided according to the degree of hairiness of the glumes. Hairiness can also be associated with stems and leaves. Probably all Linneons of cereals may be divided into forms with and without anthocyanin in the stems, and into forms with leaves and stems covered with a waxy coating and others lacking this covering.

In nearly all Linneons which have been studied there have been found forms with prostrate, and others with upright growth habits.

General Scheme of Variability in Species of the Gramineae[1]:—

	Heritable variable character		*Secale cereale* L.—Rye	*Triticum sativum* Asch. & Gr.—Wheat	*Hordeum sativum* Jessen—Barley	*Avena fatua* L.—sens. ampl.—Oats	*Panicum miliaceum* L.—Millet	*Andropogon sorghum* Brot.—Sorghum	*Zea mays* L.—Corn[2]	*Oryza sativa* L.—Rice	*Agropyrum repens* L.—Couch grass
Inflorescence	Articulation of spikelets and florets (tendency to self-sowing)	Spikelets and florets breaking apart on ripening (rachis brittle)	+	+	+	+	+	+	+[3]	+	+
		Spikelets and florets not breaking apart (rachis not brittle)[4]	+	+	+	+	+	+	+	+	+
	Hulledness	Grain hulled (tightly enclosed in glumes); not shattering on maturity	+	+	+	+	+	+	+	+	+
		Grain naked (easily separated from hull in threshing); easily shattering in ripening	+	+	+	+	+	+	+	+	+
	Compactness	Compact	+	+	+	+	+	+	+	+	+
		Loose	+	+	+	+	+	+	+	+	+
		Intermediate	+	+	+	+	+	+	+	+	+
	Sexuality	Dioecious	+[5]	..	..	..	..	..	+	..	..
		Monoecious	+	+	+	+	+	+	+	+	+

[1] +: Occurrence of the character in some forms of the species.
[2] Including variations in both ear and tassel.
[3] In teosinte, *Euchlaena mexicana*, which gives fertile hybrids with corn, and in such hybrids.
[4] Also in rye, barley, wheat, and a number of species of *Aegilops*, there is a type with separation of only the upper part of the glume (type of *Aegilops cylindrica*).
[5] Found by V. F. Antropova in breeding cultivated rye (1930).

In a large number of Linneons the phenomenon of vivipary[28] has been observed. Duval-Jouve in his old paper (*l.c.*) gives many examples of similarity in variation in the different genera of wild grasses (*Poa, Festuca, Bromus, Brachypodium, Agropyrum*). Even rare characters which are supposed to be restricted to certain Linneons, on detailed study become evident in other genera. For example the specific character of certain cultivated barleys—the presence of an appendage on the upper glume (*trifurcatum* type)—has recently been found in soft, hard, and English wheat, and also, to a certain extent, in rye.

If we make a detailed comparison of the characters which distinguish heritable forms in wheat and rye with those distinguishing races of other

[28] Penzig. Teratologie, 2nd edition. 1920.

Gramineae, we can see clearly the striking resemblances in the directions of variation of these characters.

The accompanying scheme of variable characters in grains and grasses is far from complete. We distinguish varieties of wheat, barley, rye, oats, corn, and sorghum by several hundreds of characters. Nevertheless, the inventory given shows the great variability within the limits of Linneons of the grain and grass family and the regularities of their appearance. Many of these characters are independently inherited, and thus they may be combined in many

	Heritable variable character		*Secale cereale* L.—Rye	*Triticum sativum* Asch. & Gr.—Wheat	*Hordeum sativum* Jessen—Barley	*Avena fatua* L.—sens. ampl.—Oats	*Panicum miliaceum* L.—Millet	*Andropogon sorghum* Brot.—Sorghum	*Zea mays* L.—Corn	*Oryza sativa* L.—Rice	*Agropyrum repens* L.—Couch grass
Inflorescence	Awnedness	Spikelets awned	+	+	+	+	..	+	..	+	+
		Spikelets awnless	+	+	+	+	+	+	+	+	+
		Spikelets short-awned and semi-awned	+	+	+	+	+	+	..	+	+
		Spikelets with deformed awns (*furcatum* type)	+	+	+	..	..	..	..	..	..
		Spikelets with awnlike appendages	+	+	+	..	..	..	..	..	..
	Character of awns	Coarse	+	+	+	+	..	+	..	+	+
		Fine	+	+	+	+	..	+	..	+	+
		Barbed	+	+	+	+	..	+	..	+	+
		Smooth	..	+	+	+	..	..	..	+	..
	Number of florets in a spikelet	One floret	+	+	+	+	+	+	+	+	..
		Two florets	+	+	(+)	+	+	+	+	+	+
		Several florets	+	+	..	+	..	..	..	..	+
	Color of glumes	White (straw-yellow)	+	+	+	+	+	+	+	+	+
		Red	+	+	+	+	+	+	+	+	+
		Brown	+	+	+	+	+	+	+	+	+
		Gray (black)	+	+	+	+	+	+	+	+	+
		Violet (anthocyanin)	+	+	+	+	+	+	+	+	+
	Hairiness of glumes	Hairy	+	+	+	+	..	+	+	+	+
		Smooth	+	+	+	+	+	+	..	+	+
	Rachis	Simple	+	+	+	..	..	..	..	+	+
		Branched	+	+	+	+	+	+	+	+	+
	Hairness of rachis	Very hairy	+	+	+	+	+	+	+	+	+
		Smooth	..	+	+	+	+	+	..	..	+
		Slightly hairy	+	+	+	+	+	+	+	+	+
	Waxy layer on glumes	Present	+	+	+	+	+	+	+	+	+
		Absent	+	+	+	+	+	+	+	+	+

thousands of heritable combinations. A knowledge of the theory of variation within the limits of given genera or species indicates the direction of variation in other Linneons and genera.

The Canadian graminologist, MALTE, has analyzed a number of heritable variations in wild grasses of North America, and has written: "The similarity in the nature of variation of several characters is, indeed, so remarkable that one cannot but agree with VAVILOV that it expresses not merely simple parallelism, but real homology of variation, having its basis in the phylogenetic constitution of the whole family. In other words, the parallelism is so conspicuous that it most decidedly points to a universal law of homologous variation.

"The recognition of such a law gives the systematist a rather definite and solid basis to work from, when the taxonomic values of the characters affected are under consideration. It simply means that within the family of *Gramineae,* all variations of the same nature ought to be considered as equal, *i.e.,* ought to be conceded equal taxonomic rank and value.

"Applied to *Agropyron* the inference is clear. The presence or absence of pubescence and awn on the lemma cannot be considered of any greater taxonomic value in *Agropyron* than in other genera of *Gramineae.*" (Pages 31-32).[29]

	Heritable variable character		*Secale cereale* L.—Rye	*Triticum sativum* Asch. & Gr.—Wheat	*Hordeum sativum* Jessen—Barley	*Avena fatua* L.—sens. ampl.—Oats	*Panicum miliaceum* L.—Millet	*Andropogon sorghum* Brot.—Sorghum	*Zea mays* L.—Corn	*Oryza sativa* L.—Rice	*Agropyrum repens* L.—Couch grass
Grain	Color	White	+	+	+	+	+	+	+	+	..
		Green (gray-green)	+	+	+	1	..	+	+	+	+
		Black (dark gray)	+	+	+	+	+	..	+	+	+
		Violet (anthocyanin)	+	+	+	..	..	+	+	+	..
	Form	Round	+	+	+	+	+	+	+	+	..
		Elongate	+	+	+	+	+	+	+	+	+
	Size	Large	+	+	+	+	+	+	+	+	+
		Small	+	+	+	+	+	+	+	+	+
	Consistency of grain	Vitreous	+	+	+	+	+	+	+	+	+
		Mealy	+	+	+	+	+	+	+	+	+
		Waxy (reacting with iodine in contrast to preceding types)	..	(+)	+	..	2	+	+	+	..
Vegetative characters	Leaf structure	Leaves with ligula	+	+	+	+	+	+	+	+	+
		Leaves without ligula	+	+	+	+	+	..	+	+	..
	Stem structure	Hollow	+	+	+	+	+	+	..	+	+
		Solid	+	+	..	3	..	+	+	..	+
	Color of seedlings	Violet (with anthocyanin)	+	+	+	+	+	+	+	+	+
		Green	+	+	+	+	+	+	+	+	+
		Variegated (with white bands)	+	+	+	+	..	+	+	+	+
	Form of growth	Upright	+	+	+	+	+	+	+	+	+
		Sprawling	+	+	+	+	+	+	+	+	+
	Hairiness of stem below the inflorescence	Smooth	+	+	+	..	+	+	..	..	..
		Hairy	+	+	+	..	..	..	+	..	..

1 In *Avena strigosa* Schreb.
2 Waxy forms found in Japanese investigations in *Panicum frumentaceum* and *Panicum italicum.*
3 In *Avena byzantina* Koch have been found forms with very thick-walled straw.

The family most closely related to the *Gramineae,* the *Juncaceae,* as shown by DUVAL-JOUVE is characterized in general by a series of forms similar to those in the *Gramineae.*

Papilionaceae.—Similar variations characterize the whole family of legumes. A detailed study of variability of different genera of this family has brought out uniformities in their differentiation into varieties, including many characters of the seeds, pods, blossoms, and vegetative organs. For example, if we compare differentiation into varieties in the above-mentioned section *Vicieae,* in-

[29] MALTE, M. O. The so-called *Agropyron caninum* (L.) Beauv. of North America. Annual Report (1930). National Museum of Canada, Ottawa, 1932.

cluding lentils, vetch, peas, grass peas, and chick peas, with differentiation in clovers, belonging to the section *Trifolieae* (*Trifolium pratense, Medicago sativa*), with the section *Loteae* (*Lotus corniculatus*), the section *Galegae* (*Caragana arborescens*) and the section *Phaseoleae* (*Phaseolus vulgaris, Soya hispida*), one cannot help noting the clear-cut resemblances in the direction of variability according to the color of seed from white to black, the number of flowers from one to five, the color of the cotyledons, the form of the seed, the color of the blossom, the form of the fruit, the structure of leaf and blossom, the hairiness of stems and leaves, the color of seedlings, and a great many other characters. Despite the specificity of the different genera and botanical

	Heritable variable character		*Secale cereale* L.—Rye	*Triticum sativum* Asch. & Gr.—Wheat	*Hordeum sativum* Jessen—Barley	*Avena fatua* L.—sens. ampl.—Oats	*Panicum miliaceum* L.—Millet	*Andropogon sorghum* Brot.—Sorghum	*Zea mays* L.—Corn	*Oryza sativa* L.—Rice	*Agropyrum repens* L.—Couch grass
Vegetative characters	Hairiness of leaf sheath	Smooth	+	+	+	+	+	+	+	+	+
		Hairy	+	+	+	+	+	..	..	+	+
	Hairiness of leaves	Smooth	+	+	+	+	+	+	+	+	+
		Hairy	+	+	+	+	+	..	+	+	+
	Waxy layer on stems and leaves	With waxy layer	+	+	+	+	+	+	+	+	+
		Without waxy layer	+	+	+	+	+	+	+	+	+
	Thickness of straw	Thick	+	+	+	+	+	+	+	+	+
		Thin	+	+	+	+	+	+	+	+	+
	Nodes	Hairy	..	+	.	+	.	.	+	..	.
		Smooth	..	+	.	+	.	..	+	..	..
	Height of plant	High	+	+	+	+	+	+	+	+	+
		Dwarf	+	+	+	+	+	+	+	+	+
		Medium	+	+	+	+	+	+	+	+	+
	Color of straw	Yellow	+	+	+	+	+	+	+	+	+
		Violet (anthocyanin)	+	+	+	+	+	+	+	+	+
	Color of leaves	Dark green	+	+	+	+	+	+	+	+	+
		Light green	+	+	+	+	+	+	+	+	+
	Width of leaf	Narrow	+	+	+	+	+	+	+	+	+
		Medium	+	+	+	+	+	+	+	+	+
		Wide	+	+	+	+	+	+	+	+	+
	Size of leaf	Large	+	+	+	+	+	+	+	+	+
		Small	+	+	+	+	+	+	+	+	+

sections to which they belong, we can speak of the existence of a form system for the entire family of legumes.

Cruciferae, Papaveraceae, Compositae, Pomaceae, Solanaceae, Malvaceae.—The same system of variability can be established for other families. For the crucifers E. N. Sinskaya has given a scheme of variability of species and genera in her work "On the Regularity in Variability of the Family Cruciferae" (1923) and in her paper on the various genera of this family.[80]

If we compare the forms found within the Linneons belonging to the genera *Raphanus, Brassica, Eruca, Lepidium,* and *Sinapis* with data on the variability for genera and species of the section *Hesperideae,* such as *Draba verna* and

[80] E. N. Sinskaya, "Oil and Root Crops of the Family Cruciferae." Trudi po Prikl. Bot. 19, Pt. 3, 1928.

Capsella bursa-pastoris which have been intensively studied by JORDAN, ROSEN, LOTSY, SHULL, and others, we cannot fail to note obvious similarities in the direction of variability and a general regularity in the diversity of forms. A study of "Flowers and Indicators," in those cases dealing with varieties within the different genera of the *Cruciferae,* brings out clearly the regularity in the process of differentiation of forms.

Close to the crucifers is the poppy family which, as far as may be judged from a study of poppies, celandine, and *Corydalis solida,* is characterized by a series of forms that are similar to those in species of crucifers. ZEDERBAUER established a parallel series of forms for fruits (apple, pear, quince, plum, apricot, peach, walnut, almond, and others) according to form and color of the fruit and characters of the crown of the tree, the branches, and the leaves. The series of forms were quite similar within the limits of different families and in related species.

	HERITABLE VARIABLE CHARACTER		*Secale cereale* L.—Rye	*Triticum sativum* Asch. & Gr.—Wheat	*Hordeum sativum* Jessen—Barley	*Avena fatua* L.—sens. ampl.—Oats	*Panicum miliaceum* L.—Millet	*Andropogon sorghum* Brot.—Sorghum	*Zea mays* L.—Corn	*Oryza sativa* L.—Rice	*Agropyrum repens* L.—Couch grass
BIOLOGICAL CHARACTERS	Growth habit	Winter type	+	+	+	+	..	..	..	+	..
		Spring type	+	+	+	+	+	+	+	+	..
		Semi-winter type	+	+	+	+	+	+	+	+	..
	Earliness	Late forms	+	+	+	+	+	+	+	+	+
		Early forms	+	+	+	+	+	+	+	+	+
	Ecological type	Hydrophytic	+	+	+	+	+	+	+	+	+
		Xerophytic	+	+	+	+	+	+	+	..	+
	Cold resistance	Low	+	+	+	+	+	+	+	+	..
		High	+	+	+	+	+	+	+	+	+
	Response to fertilization	High	+	+	+	+	..	..	+	..	..
		Low	+	+	+	+	..	..	+	..	..
	Character of blossoming	Open	+	+	+	+	+	+	..	+	+
		Closed	+	+	+	+	..	+	..	+	..
	Formation of albinos		+	+	+	+	..	+	+	+	..

"For horticulture,"—writes ZEDERBAUER,—"the presence of parallelism in variation has this significance, that it gives us the possibility of easily evaluating the diversity and leads to a uniform nomenclature . . . . and it shows for which forms we still need further search." (1927, p. 145).

Many genera in the composite family bring out clearly the regularities in heritable variability. If we compare the forms of the hawkweed (*Hieracium*) which have been extensively studied by NAEGELI, with the numerous forms of sunflower determined by E. M. PLACHEK in Saratov and COCKERELL in the United States, and also with the varieties of safflower which have been carefully studied by A. I. KUPTSOVA in Russia, and the HOWARDS in India, we can note marked tendencies in the differentiation of species. Dahlia, cornflower, chrysanthemum, aster, and chickory show similar series of variations in form and color of blossoms. In looking over the catalogues of the horticultural literature with their displays of color, we can observe an almost endless number of factors of similarity in variation in the different species belonging to the most diverse

genera of composites. This similarity shows not only in external features, but also in anatomical characters. Thus in many composites the seed coat has a layer of dark-colored cells which protect the seed from injury by the larvae of the sunflower moth. The color of the plastids in the flowers of the sunflower, safflower, and hawkweed vary similarly in the different species.

Homologous variability characterizes the nightshade, cucurbit, and mallow families, and we may suppose all of the families included in the plant world.

General Scheme of Variability in Species of the Papilionaceae:—

		Heritable variable character	*Pisum sativum* L.—Pea	*Vicia sativa* L.—Vetch	*Vicia faba* L.—Broad-bean	*Lens esculenta* Moench.—Lentil	*Lathyrus sativus* L.—Grass pea	*Cicer arietinum* L.—Chick pea	*Glycine hipida* Max.—Soybean	*Phaseolus vulgaris* L.—Bean	*Canavalia gladiata* DC—Canavalia	*Stizolobium hassjoo* Piper—Velvet bean	*Cajanus indicus* Spreng.—Pigeon pea	*Medicago sativa* L.—Blue alfalfa	*Trifolium pratense* L.—Red clover	*Lotus corniculatus* L.—Bird's foot trefoil
Blossom characters	Color of blossom	White	+	+	+	+	+	+	+	+	+	+	..	+	+	+
		Rose	+	+	+	+	+	+	+	+	+	..	..	+	+	..
		Red	+	..	+	..	+	+	..	..	..	..	..	+	+	..
		Violet-blue	+	+	+	+	+	+	+	+	+	+	..	+	+	..
		Yellow	+	..	+	..	..	+	..	..	..	..	+	+	..	+
		Variegated														
		Color of standards quite different from color of wings	+	+	+	..	+	..	+	+	..	..	..	..	..	..
		Wings and standard spotted or striped	..	+	..	..	+	..	+	..	..	..	+	+	..	+
	Size of blossom	Large	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Small	+	+	+	+	+	+	+	+	..	..	+	+	+	+
Fruit characters	Structure of pod wall	With parchment layer	+	..	+	..	..	..	..	+	+	+	..	..	..	..
		Without parchment layer	+	+	+	+	+	+	.	+	..	..	+	..	..	..
	Form of pod	Linear	+	+	+	..	+	..	..	+	+	+	+	..	..	+
		Rhombic	..	+	+	+	+	+	..	..	..	..	..	+	..	..
		Crescent shaped	+	+	+	..	..	..	..	+	..	+	..	..	..	..
		Sword shaped	+	..	+	..	..	..	..	+	+	+	..	..	..	..
		Bead-like	+	+	+	..	..	..	..	+	..	+	+	..	..	..
		Hairy	..	+	+	..	+	+	+	+	..	+	+	..	..	..
		Smooth	+	+	+	+	+	..	..	+	+	..	+	..	..	+

A striking example of parallel variability in different genera of conifers has been given by ZEDERBAUER.

* * * * *

In summarizing the regularities detailed above, we can come to the following conclusions:

1. *Species and genera that are genetically closely related are characterized by similar series of heritable variations with such regularity that knowing the series of forms within the limits of one species, we can predict the occurrence of parallel forms in other species and genera. The more closely related the species and Linneons in the general system, the more resemblance will there be in the series of variations.*

2. *Whole families of plants in general are characterized by definite cycles of variability occurring through all genera and species making up the family.*

The Prediction of the Existence of New Forms.—The regularities in polymorphism of closely related species and genera make it possible to predict the

possibility of finding corresponding forms in nature or obtaining them artificially by means of mutation, inbreeding, or hybridization. We have given examples of such prediction and its later confirmation in cases of rye and wheat without ligulae, hairy rye, and awned and awnless rye. Many times we have been successful in predicting the existence of forms that had not previously been known, on the basis of the Law of Homologous Series. We will give a few examples.

Soft wheats and related species with 42 chromosomes have forms with awned spikelets and others with awnless spikelets. There are also known

	Heritable variable character	*Pisum sativum* L.—Pea	*Vicia sativa* L.—Vetch	*Vicia faba* L.—Broad-bean	*Lens esculenta* Moench.—Lentil	*Lathyrus sativus* L.—Grass pea	*Cicer arietinum* L.—Chick pea	*Glycine hipida* Max.—Soybean	*Phaseolus vulgaris* L.—Bean	*Canavalia gladiata* DC—Canavalia	*Stizolobium hassjoo* Piper—Velvet bean	*Cajanus indicus* Spreng.—Pigeon pea	*Medicago sativa* L.—Blue alfalfa	*Trifolium pratense* L.—Red clover	*Lotus corniculatus* L.—Bird's foot trefoil
Fruit and seed characters — Color of ripe pod	Yellow	+	+	..	..	..	..	..	+	..	..	..	..	..	..
	Green	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Violet (with anthocyanin)	+	+	..	+	+	+	+	+	..	..	+	+	+	..
	Yellow-green	+	+	..	..	+	+	+	+	+	..	+	..	+	..
	Black (dark brown)	+	+	+	+	..	+	+	+	..	+	+	..	..	+
	Spotted (striped)	..	..	..	+	+	..	..	+	..	..	+	..	..	..
Size of pod	Large	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Small	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Surface of pod	Smooth	+	+	+	+	+	+	+	+	+	..	+	..	..	+
	Tuberculate	+	+	+	..	..	..	..	+	+	..	..	..	..	..
	Convex	+	+	+	+	+	+	+	+	+	+	+	..	..	..
	Flat	+	+	+	+	+	..	+	+	+	+	+	..	..	..
Seed form	Spherical	+	+	+	+	+	+	+	+	..	+	+	+	+	+
	Oval (egg-shaped)	+	+	+	..	..	+	..	+	+	+	+	+	+	..
	Cylindrical	..	+	+	..	..	..	..	+	+	..	+	..	..	..
	Flat (disk-shaped)	+	+	+	+	+	..	+	+	+	..	+	+	+	..
	Angular	+	+	+	..	+	+	..	+	..	..	..	..	..	..
	Kidney-shaped	+	..	+	..	..	..	..	+	+	+	..	+	+	..
Seed surface	Smooth	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Wrinkled	+	+	+	..	+	+	+	+	+	..	..	..	..	..
Seed color	White	+	+	+	..	+	+	..	+	+	+	+	..	..	..
	Yellow	+	+	+	+	+	+	+	+	+	..	+	+	+	..
	Green	+	+	+	+	+	..	+	+	..	..	+	+	+	..
	Gray	+	+	..	+	+	..	+	+	..	..	+	..	..	..
	Rose	+	+	+	+	+	+	..	+	+	..	+	+	..	..
	Red (terra-cotta)	+	+	+	+	+	+	..	+	+	..	+	..	..	..
	Brown	+	+	+	+	+	+	+	+	..	+	+	+	+	+
	Black	+	+	+	+	..	+	+	+	..	+	+	..	..	..
Variegation of seed coat	Marbled	+	+	+	+	+	+	+	+	..	+	+	+	+	+
	Punctate	+	+	..	+	+	+	+	+	..	..	+	..	..	+
	Spotted	+	+	+	+	+	+	+	+	..	..	+	..	..	..

short-awned forms of soft wheat, and peculiar furcate forms with inflated glumes and awn-like appendages. Until recently, among the hard wheats (*T. durum*) and the English wheats (*T. turgidum*), awnless or furcate forms had not been known. The existence of such forms could be predicted because of the general occurrence of this variation in grains and grasses. Our investigations in Abyssinia in 1927 led to the discovery of awnless hard and English wheats, and also to the finding of short-awned and inflated forms of the same species. In addition the group of hard and English wheats from Abyssinia included numerous characters which occur in soft wheat, for example, hairy leaves and susceptibility to leaf rust.

Thus were determined striking similarities between hard and soft wheats which are quite distinct in their numbers of chromosomes.

The species *Triticum vulgare, T. compactum, T. spelta, T. dicoccum, T. monococcum,* and *T. turgidum* contain both winter and spring forms. The hard wheats (*T. durum*), despite their great variability, until recently were known only in the form of typical spring varieties. In the literature, to be sure, there were reports on the existence of a winter form of hard wheat, but they were contradicted by other workers. *A priori,* we might expect to find winter forms

	Heritable variable character		*Pisum sativum* L.—Pea	*Vicia sativa* L.—Vetch	*Vicia faba* L.—Broad-bean	*Lens esculenta* Moench.—Lentil	*Lathyrus sativus* L.—Grass pea	*Cicer arietinum* L.—Chick pea	*Glycine hispida* Max.—Soybean	*Phaseolus vulgaris* L.—Bean	*Canavalia gladiata* DC—Canavalia	*Stizolobium hassjoo* Pi-per—Velvet bean	*Cajanus indicus* Spreng.—Pigeon pea	*Medicago sativa* L.—Blue alfalfa	*Trifolium pratense* L.—Red clover	*Lotus corniculatus* L.—Bird's foot trefoil
Seed characters	Color of Cotyledons	Green (gray)	+	+	..	+	..	..	+	+	+	+	+	..	..	+
		Yellow	+	+	+	+	+	+	+	+	..	..	+	..	..	..
		Red (orange)	+	+	..	+	..	..	..	+	..	..	..	..	..	..
	Seed size	Large	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Small	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Color of scar	White	+	+	+	+	+	+	+	+	+	+	+	..	..	+
		Brown	+	+	+	+	+	..	+	+		.	..	..	..	..
		Black	+	..	+	+	..	..	+	+	+	.	..	..	..	..
Leaf characters	Leaf structure	With tendrils	+	+	..	+	+	..	..	..	..	..	..	..	..	..
		Without tendrils	+	..	+	+	..	+	+	+	+	+	+	+	+	+
	Leaf form	Linear	..	+	.	+	+	..	..	..	..	..	..	..	..	+
		Wedge-shaped	+	+	+	..	..	..	+	+	.	..	..	..	..	..
		Oval	+	+	+	+	+	+	+	+	+	+	+	+	..	+
	Size of leaf	Long	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Short	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Wide	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Narrow	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Leaf margin	Entire	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Toothed	+	+	+	..	..	+	..	..	..	..	..	+	..	..
	Hairiness of leaves	Hairy	..	+	..	+	..	+	+	+	+	+	+	+	+	+
		Smooth	+	+	+	..	+	..	..	..	+	..	..	+	+	+
	Color of stipules	Green	+	+	+	+	+	+	+	+	+	+	..	..	..	..
		With anthocyanin	+	+	+	..	+	+	+	+	+	..	..	..	..	..
	Color of leaves	Yellow	+	+	..	+	..	+	+	+	..	..	..	+	+	..
		Green	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Waxy layer on plant	With waxy layer	+	+	..	..	+	..	..	..	..	..	..	..	..	..
		Without waxy layer	+	+	..	+	+	+	+	+	+	..	+	..	..	+

of hard wheat. D. D. Bukinich has actually found these in the Sumbarsk region at the edge of Iran and Turkmenia.

Wild barley, *Hordeum spontaneum,* was known only in the form of winter varieties. In collections made in Afghanistan, in Iran, and in Turkmenistan there have been found spring varieties of this barley. Until recently, botanists the world over did not know of hull-less winter barleys. Theoretically these might have been predicted. In 1934 they were found in a great number of forms from China and Japan. As we have seen above, many species of cereals are characterized by having both hulled and hull-less forms, as in oats, wheat, barley, and corn. Such forms were later found in millet.

On the basis of the Law of Homologous Series there have been found forms of lentils with green cotyledons.

Soybeans usually consist of forms with hairy pods. *A priori,* we might expect to find forms with smooth pods. Such forms were actually found by us in materials in the University of Illinois which originally came from Japan and Manchuria.

Squashes and cantaloupes are characterized by having forms with simple and others with segmented fruits. In the literature there were not known to exist segmented forms of watermelon. Such forms, however, were found in investigations in the southeastern European part of SSSR.

	Heritable variable character		*Pisum sativum* L.—Pea	*Vicia sativa* L.—Vetch	*Vicia faba* L.—Broad-bean	*Lens esculenta* Moench.—Lentil	*Lathyrus sativus* L.—Grass pea	*Cicer arietinum* L.—Chick pea	*Glycine hispida* Max.—Soybean	*Phaseolus vulgaris* L.—Bean	*Canavalia gladiata* DC—Canavalia	*Stizolobium hassjoo* Piper—Velvet bean	*Cajanus indicus* Spreng.—Pigeon pea	*Medicago sativa* L.—Blue alfalfa	*Trifolium pratense* L.—Red clover	*Lotus corniculatus* L.—Bird's foot trefoil
Stem characters	Stem structure	Straight	+	+	+	+	+	+	+	+	+	+	+	..	..	+
		Twining	+	+	..	..	..	..	+	+	+	..	..	..	..	..
	Plant height	High	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Intermediate	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Dwarf	+	+	+	+	..	+	+	+	+	+	+	..	..	+
	Hairiness of stem	Hairy	..	+	..	+	..	+	+	+	+	+	+	+	+	+
		Smooth	+	+	+	..	+	..	..	..	+	..	..	+	+	+
	Form of stem	Cylindrical	..	+	.	..	..	+	+	+	+	+	..	..	+	..
		Four-sided	+	+	+	+	+	+	..	+	..	..	+	..	+	+
		Fascia-like	+	..	..	+	..	..	+	..	..	..	+	..	+	+
	Color of shoots	Green	+	+	..	+	+	+	+	+	+	+	+	+	+	+
		With anthocyanin	+	+	..	+	+	+	+	+	+	+	+	+	+	+
	Color of stem	Green	+	+	..	+	+	+	+	+	+	+	+	+	+	+
		Violet (with anthocyanin)	+	+	..	+	+	+	+	+	+	+	+	+	+	+
	Habit	Erect	+	+	+	+	+	+	+	+	+	+	+	+	..	+
		Decumbent	+	+	..	+	+	+	+	+	..	+	+	+	..	+
Biological characters	Vegetative period	Early	+	+	+	+	+	+	+	+	+	+	+	+	+	+
		Late	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Formation of albinos	Present	+	+	+	+	+	+	..	+	..	..	..	+	+	..

All ordinary cantaloupes are characterized by having creeping vines which are unsuitable for row cultivation. It could be predicted that in the places where varieties have been differentiated, there might be found cantaloupes with upright growth. Such were actually found in northern Afghanistan in 1924.

Investigations of African, American, and Asiatic cottons carried out in recent years on the basis of the Law of Homologous Series have disclosed many new and earlier unknown forms, and have revealed a striking parallelism in the diversity within different species of *Gossypium.*[81] We might say that each new expedition has confirmed the applicability of the Law of Homologous Series in plant explorations. The species *Gossypium arboreum, G. herbaceum, G. hirsutum, G. purpurascens,* and *G. barbadense* show almost complete parallel

[81] See S. G. Zaitsev on "The Classification of the Genus Gossypium," Trudi po Prikl. Bot. 18, Pt. 1, 1927, and also S. E. Harland, "Genetics of Cotton." Bibliographia Genetica. 1932.

series of forms according to morphological, and to some extent physiological, characters.

Finally we can give still further examples. In wheat, rye, corn, and oats there are forms with eligulate leaves. Such forms appeared to be lacking only in barley despite special searches carried out by us in different regions during the past ten years.

Theoretically, on the basis of the Law of Homologous Series, such forms should either exist in nature or be produceable artificially, as through mutations.

By using X-rays, very recently A. N. LUTKOV in the Institute of Plant Industry, has succeeded in obtaining awnless forms of barley, and has thus supplied one of the missing links which has long concerned investigators.

In our investigations of the race constitution of cultivated plants, we have adhered to a system worked out on the basis of the Law of Homologous Series of Heritable Variations, which make it possible to determine many forms that by other means, in many cases, would fail to come to the attention of the systematists.

As the investigations have expanded more widely and deeply, there has evolved the system of homologous series in families, and there is no doubt that the determination of such series and systems will not only reveal missing links in the chain of relationships, but will develop particularly with respect to physiological, anatomical and biochemical characters.

4. **Phenotypic and Genotypic Variability:**— Up to this point we have been speaking about the existence of phenotypic variations—Jordanons, Linneons, genera, and botanical families, in the sense of Johannsen, appear to be phenotypic. It is very probable that in some degree the same rules apply to genotypic variations. The majority of the differences given above, on the basis of which systematics is built, are unquestionably hereditary and are displayed under uniform conditions. Under such conditions the different phenotypes depend on genotypic differences. However under uniform environment and otherwise comparable conditions, there can sometimes be demonstrated different genotypes, as has been shown by the investigations of present-day genetics. We know that red color in the grain of wheat can be conditioned by one, two, or three genes (NILSSON-EHLE), and yellow cotyledons in peas may be of either dominant or recessive types. Awnedness in wheat may be either recessive or dominant. Unfortunately, the genetic investigations, even of cultivated plants, are still only at a beginning. The genetics of different plants will give but a fragmentary picture, even for the best studied plant objects.

Genetic investigations force us to be cautious and not always to judge by external appearance, but to have regard for the genetic constitution. HARLAND has shown that different species of cotton, which show striking homologous series both morphologically and physiologically, may be very unlike with reference to their genes, particularly gene modifiers.[32]

As to the probability of genetic differences in similar-appearing phenotypes, there are indications of this in polyploids with double or quadruple the normal chromosome number, which are rather common among plants (wheat, oats, roses, and poppies). It is possible that polyploidy may condition the polymeric nature of some plant characters (in the sense of LANG and NILSSON-EHLE).[33]

[32] S. E. HARLAND. "The genetic conception of species." Dokl. Akad. Nauk. SSSR. 1933. 3. XI.

[33] E. I. BARULINA. "Comparative-genetic studies of species of *Triticum*." Trudi po Prikl. Bot., Series II, No. 5, 1933.

Thus phenotypic investigations are the first stages through which genetics investigations must pass.

Proceeding from the striking resemblance in genotypic variation among species within a given genus or closely related genera, conditioned by identical evolutionary processes, we must assume the presence in them of many common genes along with genes that are specific for the species and genera. Many facts indicate the presence of similar basic genes in closely related species and genera. Mutation in such genera and species, as is well known, proceeds in the same directions. MORGAN, BRIDGES, STURTEVANT, WEINSTEIN, and MULLER have determined this for different species of *Drosophila*, BABCOCK for walnuts, and DE VRIES, GEITZ, STOMPS, and others for *Oenothera*. In different species of rodents there have been demonstrated identical genes (at least so far as regards external effects and behavior).

The homologous genes that have been best studied genetically are in *Drosophila melanogaster* and *D. simulans*. In this case it has been precisely shown, by crossing experiments and a study of the localization of genes in the chromosomes in both species, that there are no less than 26 common genes, located in identical positions in corresponding chromosomes (STURTEVANT, 1929). This is the best-studied genetic example of homologous variability in two related species.[84] For other species of *Drosophila* the presence of homologous genes has not been demonstrated because of difficulty in crossing the species.

The next best-studied example, which is far removed from the preceding one, is the genotypic constitution of wild flax, *Linum angustifolium* and cultivated flax, *L. usitatissimum*, investigated by TINE TAMMES.[85]

The genetic constitution of the characters for color of blossoms, pods, seed, and stems in the best investigated legumes: peas, lentils, sweetpeas, and others—shows a clear-cut resemblance in genotypic structure of these genera, which is particularly apparent in the determination of dominant and recessive genes and genes which have a pleotropic effect. (See the summary on plant genetics by MATSUURA in 1933 and the data of E. I. BARULINA).

BAUR, in the 4th edition of "Einführung in die experimentelle Vererbungslehre" (1919), in the chapter on mutations, has noted a striking parallelism of mutations in different related species of plants and animals and "a notable homology of the series of mutations," as he expresses it.

In general, in comparing the mutations in related plants and animals, we can observe numerous similar types of mutations.

The process of segregation after hybridizing wheats with different chromosome numbers, and using different combinations of species, shows a great parallelism appearing in similar forms: narrow-leaved and wide-leaved forms; the appearance of forms with branched heads; the development of awns on the glumes; and the appearance of dwarfs, giants, and albinos. This regularity of parallelism can not be regarded as merely accidental. It testifies to a general genetic phenomenon.

In our crosses of hull-less oats having colorless glumes and hulled forms having grey glumes, in the second generation, as well as in succeeding generations, all the plants with hull-less grain were colorless, showing a clear-cut antagonism between the genes conditioning hull-lessness and the genes for colored glumes.

The same thing was observed in crossing black-glumed barleys with yellow

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[84] STURTEVANT, A. H. The genetics of *Drosophila simulans*. Publ. of Carnegie Institution in Washington. Nr. 399. 1929.

[85] TAMMES, T. The genetics of the genus *Linum*. Bibliogr. Genetica. 4, 1-36. 1928.

or colorless hull-less forms. In addition, all the forms of hull-less millet which were found in Afghanistan and Uzbekistan were white-grained (colorless). The identity of the gene *"chlorina"* in the species *Mirabilis jalapa* and *M. longiflora* has been shown by CORRENS. Using the method of hybridization, BAUR found a number of common genes in *Antirrhinum majus* and *A. molle*.

DETLEFSEN by crossing two species of the guinea pig (*Cavia porcellus* and *C. rupescens*) found in them seven identical genes.

From the overwhelming number of facts on the similarity of heritable variations in related species and genera, from the similarity of mutations in closely related genera and species, from the data of genetics, even though they are fragmentary, and finally from the general evolutionary conception of relationship and identity in development, we may consider it a probably valid assumption that the *Law of Homologous Series is also basic for genotypes.*

5. **Formulation of the Law of Homologous Series:**— The regularities discussed above may be presented by symbols as follows. As we have seen, different Linneons and different genera show great numbers of varying forms. At the same time the range of this variability is similar in related Linneons and genera. For brevity we will designate the different variable characters by letters, *a, b, c, d, e, f, g, h, i, k,* etc. Different expressions of these characters may be designated by subscripts as a_1 a_2 a_3 a_4 . . . . b_1 b_2 b_3 b_4, etc. For example the color of the glumes may be designated by the letter a; white glumes will then be a_1, yellow a_2, red a_3, grey a_4, etc.

Linneons and genera are distinguished not only by these characters, but also by specific complexes of morphological, physiological, and genetic nature. These specific differences we may call *radicals.* There can be radicals of species, genera, and whole families. Thus for three closely related Linneons of the same genus we may have the following expression of their morphological and physiological properties:

$$L_1\ (a + b + c + d + e + f + g + h + i + k\ .\ .\ .)$$
$$L_2\ (a + b + c + d + e + f + g + h + i + k\ .\ .\ .)$$
$$L_3\ (a + b + c + d + e + f + g + h + i + k\ .\ .\ .)$$

L_1, L_2, and L_3 are radicals distinguishing these Linneons from one another; *a, b, c* . . . are the varying characters, such as color and form of the glumes, leaves, stems, etc. Each of these characters can be complex in itself, and may be correspondingly divided into a greater or smaller number of morphological and physiological units: a_1, a_2, a_3, etc. Each of these morphological units may be represented in terms of its genotypic composition, in turn, if this is necessary and possible.

If we compare, for example, three Linneons of wheat, *Triticum vulgare, T. compactum,* and *T. spelta,* we may say that the radicals of these are distinguished morphologically according to the degree of compactness of heads. *T. spelta* is distinguished from the other species also by the tightness with which the grain is enclosed in the spikelet. The varying characters of varieties will be uniform in all these Linneons.

The radicals of the species *Triticum vulgare* and *T. durum* are distinguished primarily by the number of chromosomes (42 and 28).

The same may be done with different genera. Let us consider rye and soft wheat. As we have already seen, these are comparatively close in the similarity of directions of variability. Although at first glance it appears that there is no difficulty in distinguishing rye from wheat, nevertheless, there are actually very few characters specific for each of these genera. The other characters may be found, although sometimes in rare varieties, in both species. In

other words there are very few morphological characters in this case which can be represented outside the parenthesis in constructing the radical. We designate the radicals of different genera by letters: G_1, G_2, G_3, etc. If we indicate the formulas for the constitution of rye and soft wheat, we obtain the following:

$$G_1\ (a + b + c + d + e + f + g\ .\ .\ .)$$
$$G_2\ (a + b + c + d + e + f + g\ .\ .\ .)$$

The characters indicated within the parentheses are more or less identical in the two species. The principal differences from the morphological point of view in this case are differences in the glumes of rye and wheat and also in the characters of the grain. Rye has 14 chromosomes. Soft wheat, with which we are comparing rye, has 42 chromosomes. Other generic characters are less clear and less stable. Since many genera include a significant number of Linneons, a more correct representation of the genus would be the following formula:

$$G_1\ [(a + b + c + d + e + f + g + h\ .\ .\ .)\ L_1, L_2, L_3, L_4, L_5]$$

The conceptions of "radicals" for Linneons and genera, in view of our present day inadequate knowledge, must be abstract conceptions, to a considerable extent, but with the passing years the conceptions become less abstract and more and more materialistic. In many plants, for example in species of wheat, oats, barley, millet, cotton, and tobacco, the conception of "radical" must include a consideration of the chromosome numbers in the species, making it possible to divide these into short series.

Species of vetch (*Vicia*) and cotton (*cf.* Scovsted) are well distinguished according to the morphology of their chromosomes.

Many species of plants are sharply distinguished by the presence of specific chemical components (ethereal oils, acids, alkaloids).

Even though comparatively abstract, because of our deficiencies in knowledge, the concept of radicals is convenient for systematics, since it forces investigators to concentrate their attention on the substance of generic and specific differences.

The recurrent series of forms in different species, and all the more in different genera, along with the homologies, clearly indicates that there are certain *specific* features in the external manifestations of a given character which are combined, in the different radicals, into general complexes of the genera or species. Similar characters appear in their own manner to a recognized extent. For example, the series of forms according to awnedness of the heads in different species of wheat and barley with different chromosome numbers show, on the whole, a striking parallel—a fully homologous series, but at the same time each species and genus shows certain specific differences in details. The same is observed in turnips (*Brassica rapa* and *B. napus rapifera*) and radish, with respect to color of the root and fruit. All three species have colored forms giving a homologous series, but all show certain details of difference in the color. Even a homologous gene which appears in different radicals and different genotypes may show peculiarities in the different cases.

If, from this point of view, we consider the distribution of different plants in Linnean species and genera, we must note that in many cases this distribution follows systematics quite regularly, whether we are considering the distribution of species or the characters which make up the radicals of Linneons and genera. Some systematists, such as Linnaeus, Jussieu, de Candolle, and Boissier, were astonishingly sagacious in this regard, but in many other cases it was the other way around. Alternately varying characters were often

confused with the characters of species radicals. This was particularly frequent in those cases where new species and genera were described from plants consisting of single specimens collected in one locality. From our representation of systematic units, it is clear that in new separations into species and genera for phylogenetic purposes, we must depend primarily on the characters of radicals.

Many of the "new species" described by botanists actually are only new Jordanons. A task of the future is to revise all these doubtful species and thereby reduce the number of species.

The Regularity of Chemical Variability Within Species and Genera.—The morphology of different species and genera is associated with differences in chemical composition of the organism. Species and genera differ chemically, and it is only because of our inadequate study of such properties that we are limited to classifications based on morphological characters. As has been shown by ROCHLEDER, GRESHOFF, HALLIER, M. WHELDALE, JARETZKY, S. L. IVANOV, MOLISCH, V. I. NILOV, and others, closely related species of plants are characterized by similarities in chemical composition produced by similar or identical specific chemical compounds.

The *intraspecific* range in chemical composition, as shown by V. I. NILOV, usually involves quantitative relationships of rather constant specific chemical substances, formulas, in other words, of a quantitative character. The quantitative intraspecific range may be very wide. For example, the quantity of nicotine in different varieties of common tobacco varies from a bare trace up to 11%. The quantity of alkaloids in different forms of lupin varies from 0.01 up to 2.5%. The quantity of sugar varies in cantaloupe from less than 1% to 12%. Varieties of grapes within a given species differ markedly in their acidity. At the same time, the qualitative nature of chemical substances associated with species, according to the data of V. I. NILOV, appears, at least with respect to ethereal oils and alkaloids, to be very constant and characteristic of species radicals.

It is quite another matter *within the limits of genera,* where different species are distinguished chemically not only in a quantitative, but also in a qualitative fashion, and where the different species are usually characterized by theoretically specific chemical isomers or related chemical compounds. Related genera show a rather clear parallelism in the variability of the species, and we can make use of this in searching for corresponding chemical components. Knowing the chemical variability in a neighboring genus, we can search for, or obtain synthetically within the limits of the given genus by crossing, chemical substances of a specified nature.

On the whole this regularity is very clear and the chemical study of more and more genera and species of plants, in turn, confirms more and more the presence of this kind of regularity, and this has practical value for the purpose of discovering needed components. However, it is necessary to have in mind that there are exceptions, although they are not frequent. For example caffein is present not only in *Coffea arabica* and in *C. liberica* which belong to the family *Rubiaceae,* but also in the Chinese tea plant *Thea chinensis* in the family *Theaceae,* in the kola-nut—*Sterculia acuminata* and *S. vera* (family *Sterculiaceae*) and also in cacao—*Theobroma cacao* and *Paullinia sorbilis* of the family *Sapindaceae,* and in the Paraguay holly, *Ilex praguayensis* and *I. vomotoria* (family *Aquifoliaceae*). In other words, specific substances such as caffein appears to be, may be found in different families. As has been correctly pointed out by H. MOLISCH, in determining relationships it is necessary to use not only chemical differences but also as many other characters as possible. "The in-

herited substance of plants is determined by many elements or genes, and hence it is not surprising that one gene or another is encountered at distant points in the classification system where it governs the formation of some given specific substance." (H. Molisch, 1933, p. 12.)

The wide range in color of various organs within the limit of a species is no doubt due to chemical differences. The intraspecific differences in chemistry of cereal pollens brought out by color reactions with iodine, the variations in structure of the endosperm within species of grains, such as corn, wheat, sorgo, and *Coix,* ranging from vitreous to mealy and waxy, and finally the gross anatomical differences which are brought out clearly by using different methods of staining, all these testify to the presence of a significant range of chemical differences within the limits of species. These differences impel us to go more deeply into chemical investigations, and, if possible, within the limits of species to discover series of chemical differences of a qualitative nature, not only in relation to ethereal oils and alkaloids, but to other components, and most of all to the proteins.

6. **Parallel Variation in Distant Families:**— We have considered variation included within Linnean species, genera, and families. Studies have shown, however, that parallel variability also appears in different families that are genetically unrelated, and even in different classes.

Albinism.—Such a phenomenon is heritable albinism, *i.e.,* the appearance of plants without chlorophyll, and semi-albinos, which occur in the most diverse families. This has been demonstrated in many genera of *Gramineae, Compositae, Papilionaceae, Chenopodiaceae, Polygonaceae, Onagraceae, Rosaceae* (peas, beans, wheat, barley, corn, raspberries, forget-me-nots, primrose, According to the degree of albinism there are distinguished the horticultural forms: argentea, aurea, variegata, albo-variegata, aureo-variegata, and argenteo-variegata.

Gigantism and Nanism.—Among the genetically most diverse and unrelated families, such as *Gramineae, Papilionaceae, Urticaceae, Solanaceae,* and *Rosaceae* (peas, beans, wheat, barley, corn, raspberries, forget-me-nots, primrose, primula, hops, tobacco, etc.) there have been observed dwarfed forms, and at the other extreme, gigantic forms.

Fasciations.—In almost all families there appears to be a tendency to the formation of fasciated or hypertrophied organs of different kinds. This phenomenon appears through all the families from the composites to *Equisetum.* We have observed it in peas, soybeans, flax, beets, sunflowers, barley, corn, wheat, buckwheat, squashes, watermelons, and in many of the crucifers.

Dwarfs, giants, albinos, and fasciated individuals are found in the entire plant world, and even appear in the animal kingdom.

Root Forms.—Along with such all-embracing types of genotypic variability there are variations that are less widespread, but nevertheless are present in many families that are genetically only very distantly related to one another.

For example, in a number of families some genera show an inclination to the formation of fleshy roots, of which we have examples in beets, radishes, turnips, and carrots. This feature is found in dozens of different families, but what is more peculiar, if we consider the forms of the root we find that varietal differences are repeated in the most distantly related families.

For example in beets (goosefoot family) there are known to be the following basic variations: in some varieties the roots may be elongate, in others cylindrical, approaching a rhomboid form in a third group, and spherical or even flattened in a fourth group. There are varieties with segmented roots.

Similar varieties have also been observed in types of turnips and in radishes, which belong to the crucifer family, and in carrots which belong to the *Umbelliferae*, *i.e.*, in very diverse families there may be uniform series of characters.

The Forms of Fruits.—The same thing may be shown in fruits of different families: for example in apples, pears, cantaloupes, tomatoes, peaches, squashes, and watermelons. In these entirely distinct plants the different varieties show similar series of variations, there being forms that are spherical, elongate, flattened, cylindrical, pear-shaped, and segmented (as in certain varieties of cantaloupes and apples).

Color of Blossoms and Fruits.—The colors of flowers are usually dependent on two groups of pigments: (*a*) yellow or red pigmented plastids, and (*b*) rose or violet anthocyanin pigments which are soluble in the cell sap. The latter anthocyanin group is often accompanied by supplementary pigments (flavones), which are closely related chemically to the anthocyanins and have a bright yellow color and are also soluble in cell sap. Series of variations in anthocyanin colors of flowers from colorless forms through bright yellow ones to dark violet and blue forms are similar in thousands of Linneons of the most diverse families. We can see this in comparing varieties of cornflower, iris, lily of the valley, columbine, flax, chickory, hyssop, forget-me-not, stocks, peas, vetch, lilac, hyacinth, tulips and others. Some of these are rarely seen, as white, rose, and red cornflowers, or rose and bright blue lilies of the valley. They are rare, just as are many minerals in nature, but they necessarily must be kept in mind in setting up systems of genotypic variations in plants.

In those cases where a single Linneon is characterized by the presence in the blossoms of both anthocyanin pigments and colored plastids, for example in dahlias and tulips, in *Cheiranthus cheiri, Viola tricolor,* and *Helianthemum vulgare,* we have more complicated but regularly uniform series of polychroism, series of plastid and anthocyanin pigments. The distribution of pigments is an orderly arrangement with well-defined types in different varieties and plants. These types are repeated in the different families.

The parallelism of variability, as regards occurrence or absence of anthocyanin pigments in different degrees and of different qualities, is observed not only in flowers, but also in fruits of many plants, such as *Atropa belladonna, Daphne, Mezereum, Fragaria vesca, Ribes rubrum, Rubus idaeus, Solanum nigrum, Vitis vinifera,* in apples, pears, and many others (see WHELDALE).

In almost all plants and species, with rare exceptions as in the cucurbit family, the varieties are divided according to presence or absence of anthocyanin in the seedlings. The same applies also to stems.

Variability in other Characters.—Species of the most diverse families are divided into varieties with hairy and smooth leaves and stems, stipules, and fruits. Almost all plants can be divided according to the compactness of the inflorescence. Many plants are characterized by varieties with upright, and others with a procumbent habit.

ZEDERBAUER has divided varieties of woody species according to the habit of the stem or trunk and branching (*cf.* forms *pendula, pyramidalis, prostrata, nana*). Such forms are encountered both in conifers and in dicotyledons, as in willow, birch, beech, walnut, apple, pear, and quince.

Thousands of Linneons contain both simple and double-blossomed varieties.

The character of regular form of flowers appears in the most diverse families having zygomorphic flowers (*Labiatae, Scrophulariaceae, Papilionaceae,* and others).

Division into winter and spring types occur in a great number of families of herbaceous plants.

A comparison of teratological phenomena in species of various families shows definite tendencies to such variations in the most unrelated species belonging to very distinct families.[86]

In general, parallelism involves organs having the same function. In the most diverse families which have very little in common between them, such as cereals, cucurbits, and legumes, we can observe series of regular variations of both morphological and physiological characters. For example, naked-seeded forms are known not only in cereals, but also in cucurbits. In the type of hairiness of the leaves and stems, in the most different families, there can be observed a regular similarity.

7. **Homologous and Analogous Variation:**— The production of organs showing parallel variations in the cases of distantly related families may be very different, not only from the standpoint of genes, but even from the morphological-embryological point of view. The resemblance of organs in such cases appears to be due not to homology, but only to analogy.

The difference between homologous and analogous organs and characters, just as that between homologous and analogous variation, is not always easily discernible. Some authors are very competent in distinguishing between homologies and analogies, such as LOTSY, but probably more others who have been occupied with questions of phylogeny are inclined to deny the existence of a difference between homology and analogy in variation. (See LOTSY, "Evolution by means of hybridization," 1916). From the morphological point of view, in most cases, racial and varietal characters, the ones which we are considering here, appear to be homologous.

After the appearance of "The Law of Homologous Series" in 1920 and its more extensive publication in English in 1922, a number of authors have indicated that it was useful, but that in their opinion the term "homologous series," should be "homoclinic series" (YU. N. VORONOV), "genoidentical," or "analogous mutations" (PLATE), or simply "parallel" or "analogous variability."

We retain our adopted term since the basis of the Law of Homologous Series is this similarity of variations in closely related species and genera which is uniform in the inheritance of variation in whole families. We are dealing not merely with a parallelism in external similarity, but with a deeper evolutionary uniformity in the inheritance of variability in related organisms. The universality of this phenomenon appears to be due to a genetic unity in the evolutionary process that underlies relationships. The most complete parallelism is found in closely related genera, or within the limits of a family.

Finally, not in all cases, particularly in different genera, are variations produced by identical homologous genes. Identical phenotypic variations can be the result of different genes. Since systematists must work with characters, and since, in the description of the varied vegetation of the whole world, we are only theoretically concerned with genes, about which we know very little, but rather instead are concerned with observable characters under the conditions of definite environments, it is more correct to speak of homologous characters.

In cases of parallelism in distantly related families or different classes, we cannot speak of identical genes even for characters that appear to be externally identical. Given organs cannot be identified, even embryologically, in distantly related families or classes.

YU. A. FILIPCHENKO (1925) has proposed the term *genotypic parallelism* to embrace characters that are primarily found in related species and genera.

[86] PENZIG. Teratologie, 1, 2 Band, 2nd edition. 1920.

In addition, he distinguishes *anatomical parallelism* which has to do with similar development of organs, and is observed in larger systematic groups. A good illustration of anatomical parallelism is seen in the investigations of A. A. ZAVARZIN who found similarities unrelated to genetic relationships in the general histological structure of analogous organs in animals of different classes.

Later (1927) YU. A. FILIPCHENKO proposed to distinguish: 1) *genotypic parallelism* based on the presence, in related species, of identical genes and similar biotypes, 2) *ecotypical parallelism* in which identical reactions of organisms to the external environment result in the appearance of series of Jordanons (ecotypes) which may be associated with either dissimilar or identical genotypic structure, and 3) *morphological parallelism* which results from identical opportunities for development in different organs; this last kind of parallelism appears in the broader systematic groups and does not concern similar genes or genotypic structure.

The assumption of COPE, JOHANNSEN, and FILIPCHENKO that the evolution of genera and generic characters has proceeded in a different fashion from that of specific characters, and may even be conditioned by particular agents of heredity which may reside, not in the nucleus, but in the protoplasm—to us and to the majority of geneticists, this appears to be unconvincing and unsupported by the data of present-day genetics.

There next arises the new and important question of the parallelism of modifications and inherited variations (see the works of B. A. KELLER and M. A. ROZANOVA) but this question has been investigated only to small extent. It does not enter here into our problem.

8. **Variation in Fungi, Algae, and Animals:**— The same regularities appear not only in the "higher," but also in the "lower" plants, as well as in animals. The well-known Swiss mycologist ED. FISCHER (1896) devoted one of his studies to the parallelism in *Tuberaceae* and gastromycetes in which he noted a striking repetition in the ascomycete and basidiomycete series. SACCARDO, in his "Sylloge Fungorum," on the basis of the Law of Analogies, has noted the existence of parallel series of forms in fungi, and on this principle has constructed an entire system of the classification of fungi.

On the whole SACCARDO's system has proven to be too artificial. It has followed basically the classification of varietal characters of "higher" plants; its subdivisions into larger groups and genera are based, not on radicals, but primarily on varietal characters. Nevertheless a beginning in this direction has great significance in systematics. N. M. GAIDUKOV has demonstrated parallel series of forms in schizophytes and algae (1926).

N. MOROZOVA-VODYANITSKAYA, in the publication "Homologous Series as the Basis for Classification of the Genus *Pediastrum* Meyen" (1925), confirmed for algae the applicability of the Law of Homologous Series and tested its application in the systematics of the genus *Pediastrum*.

The systematic division of many genera into Linneons in zoology frequently reveals clear-cut series of homologous variations. Paleontology gives many examples of this. If we look into the zoological literature and include paleontological materials on variation and systematics, we find many data on parallel variability.

The American paleontologist, COPE, in his discussion of the particular routes of evolution of genera and species, has introduced the idea of homologous series at the basis of parallelism of variability. Among the higher groups of animals, in his opinion, there may be demonstrated series of "homologs" on the same principle as for chemicals such as alcohol and its derivatives. In

mollusca, amphibia, turtles, lizards, birds, and mammals, he showed a parallelism in structure, and Cope also developed the idea of related radicals which change in evolution without changing the species.

V. M. Shimkevich (1906) developed a periodic system for the classification of pantopods which facilitated the placement of various forms and made it possible to include yet unknown forms. D. N. Sobolev determined parallel series of fossil copepods which he called in his later work (1924) "isomorphic," since at the basis of this parallelism lies an isomorphism of living substance, *i.e.*, resemblances in the structure of the substance. V. A. Dogel in classifying infusoria, arranged them in parallel series (1923). G. G. Vittenberg has used the Law of Homologous Series in constructing a periodic system of trematodes (*Cyclocoelidae*). Terentev found parallel series in amphibia, Dobrzhanskii in ladybird beetles (*Coccinellidae*) and Shvanvich in *Rhopalocera.*

J. B. S. Haldane has published an interesting paper on the genetics of color of fur in rodents and carnivora which clearly shows the similarity of genes in closely related species and genera. Even though there may be some doubt as to the identity of dominant genes in this connection, in his opinion the recessive genes are unquestionably homologous. There are particularly large numbers of similar genes in mice, rats, rabbits, and guinea pigs.

9. **The Phenomena of Mimicry and Convergence:**— The so-called phenomenon of mimicry or imitation of one species by another in form and color, which may sometimes be helpful to the species, often represents a repetition of cycles of variation in different families and genera. Mimicry may be regarded as a general phenomenon of form repetition which is characteristic of the entire organic world.

In the investigations of cultivated and wild plants, there have been found series of notable facts of mimicry in plants. Particularly interesting cases of mimicry are found in legumes. In the Saratov region there was found a flat-seeded vetch (*Vicia sativa*) contaminating the seed of lentils. Some of these forms of vetch were so similar to forms of the seed in lentils in both color and dimensions of the seed that they could not be separated out on sorting machines. The majority of such forms blossomed and ripened at the same time as lentils, and represent very typical cases of mimicry. As a result of extensive investigations of lentils and vetch (E. I. Barulina), based on a great assortment of varieties of these legumes from different regions of SSSR and Asia, there was found a striking parallelism of forms of vetch and lentils illustrated in figure 3 (front matter). It was determined that not only did vetch mimic the flat-seeded lentils, but the reverse also occurred, and there were forms of lentils, particularly from Northwest India and Afghanistan, which reminded one of the round, black-seeded typical forms of vetch with seed of the same dimensions. The resemblance of series of variations in seed of vetch and lentils was so great that even to the trained eye, it was difficult, from external appearance, to distinguish the seed of one from the other. This example appears to be an excellent illustration of homologous series in variability. The same may be seen, not only in the seed, but also in the blossoms, and many other characters of vetch and lentils. The role of natural selection in this case was very clear. Man unconsciously, from year to year, by means of the sorting machine, separated out forms of vetch which resembled the flat-seeded lentil in dimensions and form of the seed, and at the same time reproduced such forms. The appearance of flat-seeded vetch like the flat-seeded lentil, confirms the general correctness and applicability of the law of variation.

The phenomenon of mimicry, from our point of view, appears to be general

and in those cases where species and genera show a resemblance in variations and belong to the same family, we have illustrations of the Law of Homologous Variability.

In a particular category, having no relation to the Law of Homologous Series, or, in general, to parallel variability, are included cases of mimicry of organisms as regards external form, form of leaves, etc.

The phenomenon of convergence or resemblance in characters is known in many existing and fossiliferous, closely or distantly related, forms of animals and plants; we find it occurring under the same or different conditions and it also indicates parallel variability whether homologous or analogous. The number of facts on convergence of animals and plants increases each year. LINDEN has found many cases of convergence in gastropods,[37] and ALVERDES has published on the parallel development of birds and mammals.[38]

General Conclusions:— The presence of parallelism in polymorphism and the existence of regularity in the differentiation of Linneons, genera, and families, greatly facilitates study of variations of plants and animals. Investigators, instead of blindly searching, can predict the existence of forms that are lacking in a system, on the basis of resemblance of variation in related known species and genera. The investigation of polymorphism and the description of new species becomes completely scientific in significance. New forms must fill in the gaps in a system. The collection of species and varieties of animals and plants acquires new significance when the systematics is not just natural curiosity, but an attempt to understand the meaning and order of living things in the whole organization of life.

Existing systems of Linneons and varieties must be re-evaluated according to their harmony with a general plan. An important problem of systematics appears to be to work out a single system, based on specific differences of species and varieties and their radicals, along with the analysis of homologous series of variations within the limits of species.

Instead of having in mind innumerable forms named for the place where they have been found, or in honor of persons, there is opened up the possibility of developing a system of species and genera. This is a problem for biology of the future, requiring extensive differential works for the different groups of species and genera. Without such differential works there cannot be fundamental synthetic works. In order to integrate, it is necessary to differentiate. Historically this course is inevitable.

Present-day biology in its development repeats, to some extent, the developmental course of organic chemistry. Chemistry has been far ahead of biology. Innumerable chemical compounds have been grouped together in the construction of a system based on relatively few elements. However, in the last few decades genetics has been rapidly coming to the fore, and to some extent is beginning to resemble chemistry, at least the chemistry of organic compounds. Genetics has already worked out a laconic language of symbols for heritable factors determining external characters. The biologist is learning how to analyze organisms and to master the methods for synthesizing new forms.

The regularities in polymorphism of plants, determined by detailed study of the variation in different genera and families, may to some extent be compared with the homologous series of organic chemistry, for example the hydro-

[37] LINDEN, Countess M. VON. Unabhängige Entwicklungsgleichheit der Schneckengehäusen. Biologisches Centralblatt, Bd. XVIII. 1898.

[38] ALVERDES, F. Die gleichgerichtete Stammesgeschichte der Vögel und Säugetiere. Biologisches Centralblatt, Bd. 39, 1919.

carbon series (CH_4, C_2H_4, CH_2 . . .). Series of these compounds are distinct from one another, but are characterized by many common properties in the sense of forming definite cycles of compounds with definite reactions of substitution and combinations. Each individual hydrocarbon gives a series of compounds resembling those of other hydrocarbons.

In general, genera (G_1, G_2, G_3) and Linneons (L_1, L_2, L_3) of plants and animals also include homologous series of forms which might be considered to correspond to the different homologous series of hydrocarbons.

$$
\begin{array}{l}
G_1 L_1 (a + b + c + \ldots),\ G_2 L_1 (a + b + c + \ldots) \\
G_1 L_2 (a + b + c + \ldots),\ G_2 L_2 (a + b + c + \ldots) \\
G_1 L_3 (a + b + c + \ldots),\ G_2 L_3 (a + b + c + \ldots) \\
\qquad L_1 a_1,\ L_1 a_2,\ L_1 a_3 \ldots \\
\qquad L_2 a_1,\ L_2 a_2,\ L_2 a_3 \ldots \\
\qquad L_3 a_1,\ L_3 a_2,\ L_3 a_3 \ldots
\end{array}
$$

The letters a_1, a_2, a_3 indicate characters which distinguish the different forms. As we can see, the series of forms remind one of the homologous series of organic chemistry.

Besides their chemical structure, different forms of plants and animals are characterized by physical structure which is reminiscent of the system of classification of crystals. Variations in form to some extent may be grouped in geometrical schemes.

The problem of origin of species cannot be separated from the problem of variation. The occurrence of regularity in the variation of species leads us to a conception of the Linnean species as a definite complicated system consisting of parts which are connected with each other, and in which the parts and whole are mutually related.

The races and varieties which make up Linnean species cannot be regarded as mechanical isolated parts. They are of complicated structure resembling species, which is shown by the fact that experimental systematics of a single variety is often quite similar to that of a Linnean species. The complexity of species, the variations of species in time and space, the appearance of mutations, new forms as a result of inbreeding or hybridization, all contribute to the variations and mobility of the species. At the same time, as shown by present studies, the biologist is proceeding to an understanding of the species as orderly effective complexes. At any given moment a species has actual existence. The divergence of species is really a mental conception of the investigator. There is a harmony in the continuous and discontinuous character of the evolution of organisms. The evolutionary process is discontinuous in the sense of the constant movement of change, of origin and extinction, each being linked in an endless chain in which species are a system of heritable forms. The great amount of factual material which the present-day biologist has at his disposal forces him to approach the species in a dialectical fashion, and not to consider it as a fixed entity, the reflection of an act of creation, as the species was formerly regarded. "Since that time, as biology is studied in the light of the theory of evolution"—writes ENGELS in "Dialectics of Nature"—"in the domain of organic nature, one after another there disappear the hard and fast limits of classification, daily there is an increase in the intermediate links which will not yield to classification. More exact investigations throw organisms out of one class and into another, and distinguishing characters become hardly more than symbols, losing all absolute significance."

The different species of the present day are in different stages of their development, and in accordance with this, they represent complexes of very different amplitude and content. They may be divided into ecological-geographical

complexes which not infrequently are very sharply expressed and which may include subspecies, geographic races, etc.

Thus the Linnean species, in our conception, appears to be a distinct, complex, mobile, morpho-physiological system related in its origin to a definite environment and area, and in its intraspecific hereditary variability, subject to the Law of Homologous Series. The regularities described above cannot be regarded as absolute: not every species existent today must necessarily show homologous series agreeing with those of another species. The distinctness of species must be regarded as not absolute, but relative, taking into account difficulties in crossing species, non-homologous chromosomes, the appearance of new species as a result of crossing, the presence of well-marked morphological and physiological characteristics, as well as the differences in areas occupied by species.

In nature one finds, usually, some variations from the operation of this law, but at the same time the law is confirmed as a whole. The Law of Homologous Series in Heritable Variations appears to be a definite general tendency, inherent in organisms, and representing a general property of organisms.

Natural selection and external conditions have resulted in the past, and will result in the future, in the dying out of many links in the chain. The factors of isolation and distribution play a great role in the appearance of forms, and may cause incompleteness in the series of variations in species as compared with their original potentialities for variation. On the other hand, selection and external conditions, acting in the same fashion on different genera and species, may result in a uniformity in the expression of characters; for example, they might lead to the appearance of parallel series of ecotypes in different species and genera. Man has a major role in guiding the variation of cultivated plants and domestic animals by selection, use of hybridization and inbreeding, and conservation of mutations which in nature, would be lost.

The uniformity of many wild species is associated with their heterozygous condition, their cross-pollination, and the non-appearance of recessive characters. By using inbreeding and isolation, one ordinarily can disclose variations in such wild species.

The Law of Homologous Series is not arbitrary, limiting variations; on the contrary, it discloses the great possibilities of variation; it only states that, with regard to the entire system, thorough investigation of all the variations characteristic of species, reveals not a disorganized process, but a definite regularity that follows from the nature of the evolutionary process.

The Law of Homologous Series shows investigators and breeders the directions for their search. It aids in the discovery of systematic links and extends the horizon of the worker, disclosing the great amplitude of species variations. The hundreds of characters distinguishing heritable forms that are known already, can be combined in millions of forms in almost endless possibilities. The appearance in nature of odd or rare forms which at first glance might appear to be mutations proceeding in different directions, in the last analysis prove to be part of a regular process; what first appear to be accidental facts become necessary parts in the system of species. Mutations may appear to be accidental and going in different directions, but when they are brought together, they are found to follow general laws.

If there appear to be limitations in the series of variations, this is the consequence of physical limitations. Thus, forms of fruit vary from spherical to flat, cylindrical, oval, pear-shaped, or inverted pear-shaped, *i.e.*, they include essentially all of the basic geometric forms. The color of the glumes in cereals varies from colorless, straw yellow, or white, to black. In the same regular way the forms of leaves and many other morphological characters vary. The

amplitude of ecological types obviously is determined by the range of environmental conditions under which the species finds itself. In the extent of quantitative variation (to which we have given particular attention in our studies) there are definite regularities which are evidently associated with the constitution of the organs. Organs which are filled with parenchymatous tissue, such as fruits and roots, vary more than organs which have other types of structure. In intensive investigations of species, one can demonstrate a colossal diapason of variations.

The Law of Homologous Series lies at the basis of differential systematics of cultivated plants (see numerous works on the systematics of different genera and species in Trudi po Prikl. Bot., Sel., i Gen., beginning in 1923). It gives us the possibility of constructing a system which embraces the most diverse forms found in distantly related species divided into numerous varieties. It has been used with success in recent years in the systematics of different classes and families of plants and animals.

M. R. Levyns has used it in the systematics of the genus *Lobostemon* in the family *Boraginaceae* (1934). It has been used for algae by N. M. Gaidukov (1926) and N. Morozova-Vodyanitskaya; for grains by Malte in Canada (1932); by P. V. Terentev with amphibia (1923); by G. G. Vittenberg (1923) with trematodes; with domestic animals by S. N. Bogoylubskii (1928, 1934); and with protozoa by V. Dogel (1923).

* * * * *

In conclusion I express the firm conviction that the most rational and expedient means for studying and disclosing the system of variations in the future is the determination of parallelism in homologous series of variations. Beyond doubt this will facilitate the works of investigators in both differentiation and integration, both of which are indispensable for mastering and controlling animals and plant organisms.

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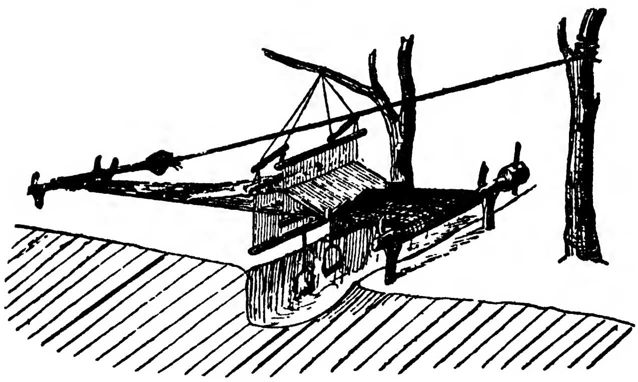
STUDY of IMMUNITY

of

PLANTS

FROM INFECTIOUS DISEASES



1. **Introduction:**— *By the term immunity we mean the lack of susceptibility of organisms to diseases.* In relation to parasitic infections, immunity indicates the impossibility for a disease-causing parasite to develop normally within a non-susceptible plant.

Among the measures for protecting plants from various diseases caused by parasitic fungi, bacteria, and viruses, and also the depredations of different insects, the most efficient appears to be the introduction of immune varieties into culture, or the creation of such by means of crossing. In relation to cereals, which occupy three-fourths of all cultivated land, the substitution of resistant forms for susceptible varieties appears to be the most practicable method for combatting such diseases as rusts, powdery mildew, loose smut of wheat, different *Fusarium* diseases, and leaf spot diseases, but even in relation to crops that are cultivated intensively, such as grape-vines or fruit trees, which are usually protected with insecticides and fungicides, here too the most practical means of combatting diseases appears to be the introduction of immune varieties.

In 1919, in the book "Immunity of Plants from Infectious Diseases," the author attempted to summarize the knowledge on the subject at that time, including the results of his own investigations.

The increase in knowledge in the field of plant immunity during this period has progressed at a geometrical rate. A more or less complete list of the world literature on plant immunity in 1919 would comprise not over 200 works, of which a considerable part only touched on the subject of immunity in passing.

At the present time the number of works on plant immunity approaches 4000.[89] In a single American journal alone, "Phytopathology," from 1918 to 1934 there were published more than 300 papers on immunity. During this interval of 15 years, the question of immunity attracted wide attention, particularly in the United States, Canada, Germany, England, France, Switzerland, Sweden, Argentina, and Italy. There have arisen new phases of the subject on which, during the past 20 years, the attention of phytopathologists, breeders, geneticists, and to some extent physiologists, has been concentrated. There have arisen new chapters in the study of immunity. There has come into being the whole science of virus diseases of plants, the significance of which is growing every year, although their biological nature, because of their submicroscopic size and filterability, has not yet been fully explained. Virus diseases have been found in several hundred kinds of plants, and the most decisive method of combatting them appears to be the breeding of immune varieties. The conceptions of parasitic species of fungi and bacteria have undergone dissociation. Investigators have studied the occurrence of various forms of parasitic fungi and bacteria. Phytopathologists have undertaken differential studies of the relationships between the external environment and the susceptibility of plants to various diseases. Studies have been conducted on the genetics of immunity. Particular attention has been given to the question of acquired immunity in plants. The studies have proceeded widely and deeply, and the significance of this field is growing every day. Whereas in 1915 even S. G. Navashin expressed doubt as to the practical possibilities in plant immunity, considering the high degree of plasticity in parasitic fungi,

[89] A complete bibliography on plant immunity may be found in the library of the All-Union Institute of Plant Industry.

today the fact of variety differences in resistance appears to be unquestionable, and more than this, it lies at the basis of governmental measures for combatting diseases. Breeders with almost every kind of plant have been working with heritable varietal differences in reaction to one or another bacterial, virus, or fungus disease, and even with differences in resistance to attack by different insects. Varietal differences in immunity have been widely used in plant breeding. The constancy of immunity has been shown for many plants. For example, in *monococcum, dicoccum,* and *durum* wheats, this has been shown to have existed for tens, and even hundreds of years.

The great amount of assembled materials, the specificity of the subject of relationships between host plants and parasites, and the uniqueness of the experimental methods in this field, give us a basis for separating out a branch of botanical science which may be called *"Phyto-immunology"* or *"Immunology of Plants."*

Among the recent extensive publications on plant immunity, besides that of E. Molz (1917), we should point out the very complete review on the interrelationships of parasites and host plants published by A. Zimmermann in 1925 and 1927 (Zentralbl. für Bakteriologie, II Abt.) embracing the literature on the *Erysiphaceae, Uredineae, Sclerotinia, Monilia,* and *Botrytis,* with particular attention to the role of environment and the nature of immunity and with a general bibliography. We should mention the book of the French investigator, Nobécourt, "Contribution to the Study of Immunity in Plants" (1927), an extensive publication dealing particularly with acquired immunity, and also the book of the Italian authors Carbone and Arnaudi, "Immunity in Plants" (1930). This last publication likewise is primarily on the question of acquired immunity. Adolph Müller has published a critical work including the results of original investigations, on the use of chemical injections of plants, "Die innere Therapie der Pflanzen," (Berlin, 1926). A very extensive treatment of the nature of resistance to parasitic diseases, and the relationship between environment and immunity is to be found in the book by Ed. Fischer and E. Gäumann, "Biologie der pflanzenbewohnenden parasitischen Pilze" (Jena, 1929). A thorough, critical study of the status of present-day knowledge on acquired and physiological immunity in plants is the publication of K. Chester (Quarterly Review of Biology, Vol. 8, 1933). The Danish geneticist H. Hansen (1934) has given us a very valuable critical literature review on the genetics of plant immunity from diseases caused by fungi, bacteria, and viruses. Valuable publications on virus diseases have been published, for example those of K. M. Smith (1933) and L. O. Kunkel (1928). The remaining extensive original literature is principally concentrated in papers in the journals devoted to phytopathology, breeding, and general agronomy. In addition, one should mention the voluminous literature in the form of bulletins of the experiment stations.[40]

[40] The most important periodical publications giving particular attention to the question of plant immunity are the following: In USA, Phytopathology (Lancaster, Pa.), Journal of the American Society of Agronomy (Geneva, N. Y.), Journal of Agricultural Research (Washington, D. C.), bulletins of the Department of Agriculture, USA (U. S. Department of Agriculture, Washington, D. C.) and experiment stations in the states of Minnesota, Kansas, Washington, North Dakota, and others; in Germany: Zeitschrift für Pflanzenkrankheiten (Stuttgart), Phytopathologische Zeitschrift (Berlin), Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten, Abt. 2 (Jena), Zeitschrift für Züchtung, Reihe A: Pflanzenzüchtung (Berlin), Der Züchter (Berlin), Arbeiten der Biologischen Reichsanstalt für Land- und Forstwirtschaft (Berlin); in England: Annals of Applied Biology (London), Annals of Botany (London); in Canada: Scientific Agriculture (Ottawa), Canadian Journal of Research (Ottawa). Recent works on plant immunity are

Unfortunately, in recent times there have not appeared any all-inclusive, critical publications on the general problems of plant immunity, particularly from the point of view of the interests of breeders.

The purpose of the present work is to attempt to give a short review of all phases of present day knowledge on immunity as applied to the problems of breeding.

First of all we will take up the question of the nature of immunity.

2. **The Nature of Immunity:**— Investigations on different plants in relation to different diseases have brought out the manifold types of resistance of plants to infections. Recent data have shown still more clearly the complexity of the nature of immunity in plants and the impossibility of referring it to simple physiological or biological causes. Basically there is found, as in animals, a division into two fundamental categories of immunity, on the one hand *natural* or *congenital* immunity, and on the other hand *acquired* immunity, produced artificially.

In distinction to animals and man, in plants natural immunity has the greater significance.

Acquired Immunity.—Acquired immunity, which has decisive significance in protecting the organism in animals and man, in plants has only limited effectiveness. Some very competent authors, for example the well-known English plant physiologist and pathologist, V. BLACKMAN, basing his conclusions on the anatomical and physiological peculiarities of plants, denied the practical applicability of acquired immunity in plants. Considering the colloidal nature of antigens, BLACKMAN did not consider sero-therapy and sero-prophylaxis possible in plants because of the transport of matter in plants which differs from that in the blood system of animals. Antigens, if they actually are formed, being colloidal substances, could not penetrate to all parts of the plant organism. In "Principles of Plant Pathology" (1928)—a detailed treatise on general plant pathology, OWENS writes on the question of artificial immunization of plants as follows: "No progress has yet been made in this direction, and it is doubtful if this ever can be done with plants, as it is done in the animal kingdom. The structure of plants is so different from that of animals, especially as regards a circulatory system, that it does not seem likely that much success can ever be attained in that direction." (See page 125.)

We are not obliged, however, to deny the theoretical possibilities of the occurrence of acquired immunity in plants. At the beginning of the 20th Century, NOEL BERNARD (1909) definitely showed that orchids, after infection with their parasitic fungus (*Rhizoctonia*), become resistant to reinfection, *i.e.*, acquire immunity.

Early in this century there were carried out experiments on artificial immunization of plants by infecting them with virulent and attenuate cultures of pathogenic organisms or by injecting them with products of bacterial metabolism or extracts of parasites. BEAUVERIE and RAY in 1901 vaccinated plants of begonia, oats, beans, and lupin with weak cultures of fungi and bacteria or even with extracts from cultures, and obtained positive results. HILTNER and STÖRMER (1903) showed that legumes infected with virulent races of nodule bacteria could not be subsequently infected with less virulent races.

referred to most frequently in the Review of Applied Mycology (Kew, England), Experiment Station Record (Washington, D. C.), Biological Abstracts (Philadelphia, Pa.), and Review of Applied Entomology, Series A: Agricultural (London). In addition, bibliographies of the principal current literature are given in the issues of the Bibliographie der Pflanzenschutzliteratur, Berlin).

In recent years interest in this field has been renewed with the publication of a number of extensive investigations which tend to confirm the findings of BERNARD and of BEAUVERIE and RAY. In 1930 the question of acquired immunity in plants was taken up at the International Congress of Microbiology in a number of contributions (CARBONE, KOSTOFF, and others).

ZOYA in Italy (1925) grew wheat in an aqueous extract of the fungus *Helminthosporium sativum* and found that the vaccinated plants showed a higher degree of resistance than the controls. The immunity was retained about a month after infection. The vaccine was still effective after heating to a temperature of 50-55° C. It was inactivated by boiling.

In France, NOBÉCOURT carried out extensive investigations on vaccination with the fungus *Botrytis cinerea* and also obtained positive results. Beans were grown in soil watered with the liquid on which the fungus had been cultured. The plants grown in this soil were inoculated artificially with the same fungus. At the same time, control plants were treated similarly, but not watered with the fungus liquid, and these died from the infection, while the experimental plants grew in the inoculated soil and remained healthy.

ARNAUDI found that branches of geranium (*Pelargonium zonale*) inoculated with *Bacillus tumefaciens* could not be infected a second time with this bacterium at a distance of three to four centimeters from the gall.

SIEDEN and TRIESCHMANN in 1926 carried out some interesting experiments producing immunity in potatoes against wart (*Synchytrium endobioticum*). They introduced into potato tubers extracts of tubers diseased with wart. The vaccinated tubers were planted in soil contaminated with this fungus. As a result the vaccinated tubers gave good yields of healthy tubers, while control, non-vaccinated tubers produced plants that were highly infected with wart.

The Italian investigators, CARBONE and ARNAUDI, carried out a large number of experiments on the immunization of plants against different pathogenic organisms, by treating them with attenuated cultures of extracts of microorganisms. These experiments, just as the older works of BEAUVERIE and RAY and the more recent ones of NOBÉCOURT, BROWN, HURSH, and ZOYA, showed that vaccination produced the development or increase in immunity in the plants. CARBONE and ARNAUDI in a monographic review published in 1930 have reported these experiments. The school of CARBONE in Milan has carried out many experiments in this field in recent times.

On the whole, numerous results from the active immunization of plants by vaccination, either with attenuated cultures of parasitic fungi and bacteria or with extracts of parasites, have had positive effect in the sense of increasing resistance. The duration of the effect of vaccination has varied in the different experiments, but in general it has not been prolonged. The nature of this type of immunization has received little study. CARBONE, as other authors, has analyzed it from the point of view of zoo-immunology.

In SSSR, work in this field has been begun in recent years in the Microbiological Institute (K. A. FRIDE and A. V. KALYAEV, A. T. KRAVCHENKO, N. I. SMIRNOVA) and in the Ukrainian Institute of Plant Protection (V. L. RIZHKOV).

In vaccinating beans by watering them with aqueous cultures of filtrates of month-old bouillon cultures of the fungus *Botrytis cinerea,* the resistance to later infection has been increased. Of the vaccinated plants, on the average 42.2% survived, while of the nonvaccinated controls only 4.3%. Anatomical investigations showed enhanced development of the cambium, protoxylem, and pericycle in the vaccinated plants.

PRICE in the Boyce Thompson Institute near New York, brought out some

interesting facts concerning the ringspot virus disease of tobacco. If tobacco plants are infected with the virus of this disease, they usually show a strong infection, but later, with further growth, they gradually recover. The leaves formed later develop without signs of disease. PRICE (1932) showed that inoculation of the leaves of such plants with the virus had no effect. If cuttings were made of the recovered parts and these were vegetatively propagated, they remained healthy on inoculation; under the same conditions control plants became strongly infected.

Other investigators have also noted that older, fully-developed leaves do not display virus attack, although these leaves may be carriers of virus.

In conclusion, the investigations of PRICE only indirectly touch on the subject of acquired immunity; they do not essentially demonstrate its presence in plants.

THUNG (1931) found that a mixture of the virus of ordinary tobacco mosaic (JOHNSON's tobacco virus 1) and the virus of white mosaic (JOHNSON's tobacco virus 6) produced in inoculated tobacco plants symptoms of one or the other disease which diminished with the growth of the plant.

If tobacco was inoculated with white mosaic virus and then with the ordinary mosaic virus, this second disease did not develop. The same thing occurred in the reciprocal order of inoculation. In other words the presence of either virus in the tissues protected the plants against infection with the other virus.

The well-known English potato specialist, SALAMAN (1933), demonstrated the same phenomenon in relation to virulent and weak strains of potato Virus X, finding that plants of tobacco or Jimson weed which were already infected with a weak strain of Virus X did not show symptoms of later infection with a virulent strain of Virus X.

The question of *antibodies, i.e.,* compounds of a protein nature in plants, produced actively on infection, analogous to those that occur in animals, has attracted particular attention. To it has been devoted a series of works in recent times (see SILBERSCHMIDT, CHESTER, WHITAKER, KOSTOFF, CARBONE, ARNAUDI, and others). The cytological picture of the relationship between parasitic fungi and the tissues of the host plant, and the symbiotic phenomena which are common in relationships between fungi and host plant cells, which will be discussed in a later chapter, testify to the probability of the production in plant cells of specific compounds—antigens and antitoxins. This is also suggested in the above-mentioned works on the appearance of immunity in plants on repeated inoculation with a given parasite. The opinion that there is a production of antibodies in plant cells to protect them from parasitic fungi was expressed by MARSHALL WARD at the beginning of the 20th century.

Dr. D. KOSTOV, working with grafts of numerous species and genera of the *Solanaceae,* found that repeated grafting on stocks that had previously been grafted did not succeed, although the first time the graft was made without particular difficulty. Further investigations of the chemistry of stock and scion of such heterologous grafts, using the method of the precipitin reaction, borrowed from zoo-immunology, led KOSTOV to the determination, in the tissues not far from the point of grafting, of substances analogous to antibodies in animals: agglutinins, lysins, and precipitins. By means of the "precipitin ring reaction," and the more sensitive nephelometric method, he came to the conclusion that there were "precipitins" in stock and scion, and also substances with a lytic or dissolving effect, determined by the use of the "lytic ring" and the method of dialysis with the Ninhydrin reaction, which is a colorometric method for determining the quantity of protein substances before and after lysis. The precipitin reactions led KOSTOV to the conclusion that in some of

his grafts there were formed precipitins and lysins in the stocks and scions, that these were increased as a result of grafting, and that this increase was particularly noticeable near the place of grafting and progressively weaker with distance from it. It increased during a month after grafting and sometimes appeared to be specific. The formation of antibodies after grafting was considered by Dr. KOSTOV as indicative of an acquired immunity. The *in vitro* reactions of tissue juices of stock and scion near the place of grafting were considered due to the presence of agglutination (clumping), precipitation (the effect of precipitins), and solution (the effect of lysins).

These data have been regarded by KOSTOV and a number of other authors as particularly convincing evidence of the existence of acquired immunity in plants, and the formation of antibodies in plant cells. However, Dr. KOSTOV refrained from using the terminology of serological reactions, recognizing the *non-identity* of the phenomena of acquired immunity in plants and animals.

SILBERSCHMIDT (1931) in a study of the KOSTOV reaction, at first held a similar opinion as to the immunological nature of the phenomenon in heterologous grafts. Further investigations by SILBERSCHMIDT, however, soon led him to opposite conclusions (1932). Numerous experiments showed the non-specificity of the acquired precipitins which, as a matter of fact, KOSTOV had observed himself in numerous experiments (1929). Only in isolated cases did SILBERSCHMIDT's results agree with those of KOSTOV's experiments. In his work published in 1932, SILBERSCHMIDT denied immunization as a result of grafting as a general phenomenon, although it must be noted that he varied KOSTOV's method by using solutions of KCl instead of distilled water.

The conclusions of KOSTOV and SILBERSCHMIDT, and in part their experimental data, were subjected to serious revision by the American investigators WHITAKER and CHESTER. While not denying the theoretical possibility of the formation of antibodies in cases of parasitism, these authors showed the non-applicability to plants of the usual serological methods borrowed from zoo-immunology.

The presence of toxins, unfavorable *p*H relationships, the absence of corresponding nutrient salts, all these and many other factors having no relationship to immunology appear in one or another of the reactions in plants. Investigators of plant immunity having to do with expressed saps or fluids from macerated tissues in physiologic solutions of salts do not obtain antibody solutions, but complexes of broken-down and altered substances which have little resemblance to the living cells. Substances which are isolated in cells with their complicated structure, when they are removed by breaking the cell membranes, and dissolved, are subject to fundamental, irreparable change.

Repeating this work on a broad scale, and with additions to the graft combinations in the experiments of KOSTOV, and those of SILBERSCHMIDT which supported the views of KOSTOV, CHESTER and WHITAKER came to the conclusion that the precipitin reactions in *Solanaceae* essentially have no immunological character. They often are not associated with protein substances. The "ring reaction," a test for observing the effects of precipitins in zoo-immunology, on the basis of which KOSTOV came to the conclusions on plant precipitins, was obtained by CHESTER and WHITAKER in extracts unrelated to immunological phenomena. The precipitins, and in general the antibodies determined by KOSTOV, in the opinion of WHITAKER and CHESTER, were not of immunological nature, had no relation to acquired immunity, and may be called pseudoantibodies or pseudo-precipitins. In general, CHESTER and WHITAKER did not confirm the formation of precipitins associated with immunity, as a result of heterologous grafting of plants, and in addition to this, in their experiments

they did not confirm the fact itself of the production of acquired immunity as a result of grafting. (See CHESTER, 1933). The precipitates obtained from "pseudo-precipitins," in the majority of cases were shown to be precipitates of calcium oxalate; hence the conclusions of KOSTOV appear to CHESTER and WHITAKER to be unconvincing as regards any demonstration of the nature of inhibitory substances. They considered that a more careful analysis of the phenomenon is necessary. It may be pointed out that WHITAKER and CHESTER (1933) in their investigations used somewhat different methods than KOSTOV. Whereas the latter used fresh green materials, the aforementioned authors employed dry, pulverized plant materials. FOSTER and AVERY (1933) retested CHESTER's methods, showing that in drying, many proteins are irreversibly coagulated.

O. MORITZ, in an appendix to the book by N. P. KRENKE, "Wundkompensationen, Transplantationen und Chimären bei Pflanzen" (1933), has stated that the recent data of SILBERSCHMIDT (1933) as well as work at the Botanical Institute at Kiel where MORITZ himself worked, have not confirmed KOSTOV's conclusions. A detailed account of MORITZ's investigations has not been published.

The methods of animal serology in CHESTER's opinion hardly apply in full to the study of plant immunity. The presence in animals of a blood system makes them far more suitable for a study of antibodies than plants.

The living plant cell in CHESTER's opinion can produce, and probably does produce, antibodies, as in animal organisms, but in plants these substances do not accumulate in the cells, and are not carried about in the blood as in animals, where they may easily be demonstrated. It is impossible to arrive at conclusions regarding specific substances from expressed juice of crushed cells. Experiments on anesthesia of plant cells and with the use of the least violent ways of killing them, show that immunity in the plant cell is lost not only after it dies, but even during the time it is narcotized. "Hence"—writes CHESTER—"there is therefore, no more reason for regarding the negative results of the 'serological' tests in plants as evidence disproving the thesis of plant acquired immunity than there would be for expecting to obtain evidence as to the cytology of the apple fruit from a microscopic examination of cider." (P. 311-312, 1933).

Acquired immunity in plants, in CHESTER's opinion, *is a vital phenomenon and is more localized than in animals.* This indicates the necessity for distinct methods for its study (for example, the use of tissue cultures in artificial media). Circulating antibodies in plants, if such exist, no doubt are more limited than in the animal organisms.

The possibility of acquired immunity in plants as a result of vaccination and the effect of parasites may be considered demonstrated in the recent investigations of NOBÉCOURT in France, and the Italian investigations of CARBONE, ARNAUDI, ZOYA, and others. Meanwhile the nature of acquired immunity in plants is insufficiently explained.

Still inadequately worked out are the questions of the duration of acquired immunity in plants, its specificity, and the particulars of the nature of antigens, *i.e.,* immunizing substances. In the above-mentioned experiments of ZOYA with wheat, the effect of the acquired immunity was short. In the experiments of BENIGNI they were even shorter.

The phenomenon of anaphylaxis, *i.e.,* increased susceptibility with repeated inoculations of the same infectious principle—a common phenomenon in animals—has not yet been definitely determined in plants.

NOBÉCOURT (1928) does not consider it demonstrated for higher plants.

Theoretically this whole field of investigation is most interesting, the more so since here it is possible, although with some modifications, to use the tests of animal immunology.

MÜLLER and CHESTER recently, just as a number of authors had done earlier (SHEVIREV, MOKRZHETSKII, NORTON, and others; see VAVILOV "Immunity of Plants from Infectious Diseases," 1919), have injected the tissues of different plants with different substances for preventing diseases, and in a number of cases have obtained positive results. The injection of plant tissues to combat insects or fungus and bacterial diseases in a number of cases has given positive results. The principle of the possibility of combatting parasites by means of injecting plant tissues with various solutions may be considered fully demonstrated. The techniques of plant therapy and the wide practical application of this method are more complex matters. The author of the recent monograph on plant therapy, ADOLPH MÜLLER (1926), in a publication in 1929, showed that the practice of injecting the effective substances into plants is hardly practicable. In his opinion it is more necessary to turn one's attention to introducing such substances into the soil to induce indirect passage into the plant for the purposes of plant protection.

It is possible that in greenhouse culture, for woody plants, and possibly for treating seed against certain diseases, vaccination or injection may in the course of time find some usefulness. It is probable that the use of acquired immunity may play a greater role for perennial plants or woody species than in herbaceous annual plants. There are indications (see CHESTER) that after heavy infection of the coffee tree with rust (*Hemileia*) and red cedar (*Gymnosporangium*), in succeeding years the effect of the parasite is significantly lessened, *i.e.,* the trees may have acquired immunity. The same thing has been noted for oak in relation to powdery mildew and for chestnut with respect to *Endothia.*

It is premature to speak at present of wide possibilities in the practical uses of acquired immunity in plants. This field still requires considerable experimental and theoretical work before putting it to practical use.

The possibility of artificially creating immunity in animals and man has opened up the widest perspectives and has led to a series of extremely important discoveries in this field. "No such great practical advantage can be prophesied for an application of acquired immunity in plants," writes CHESTER in the conclusion of his work cited above (1933)—"because of the inherent difference in the purposes of plant and human pathology. The aim of human medicine is to preserve the individual; the phytopathologist, on the other hand, as a rule has little interest in the individual, his main objective being the preservation of the population. Moreover, while much of the activity of the physician is devoted to cure or therapy, that of the phytopathologist is more directly concerned with the prevention or prophylaxis" (page 314).

3. **The Nature of Congenital Immunity:**— The occurrence of congenital immunity in varieties, as has been made clear during the past decade, embraces essentially all species and genera of herbaceous and woody crop plants, and is shown in varying degree in relation to the most diverse fungus, bacterial, and virus diseases, and also to injurious insects. Particularly numerous investigations have been carried out on immunity in cereals, potatoes, sugar beets, sugar cane, grapes, tobacco, apples, pears, and citrus fruits. The phenomena of congenital immunity are very diverse in nature, and require classification.

Practically, we may first distinguish ***the categories of immunity and resistance in relation to specialization of the parasite.*** The most important factor determining the occurrence of immunity and resistance to fungus, bacterial,

and virus diseases, and also to insects appears to be *biological specialization* of parasites on hosts—species and genera of plants. Species and genera of fungi, bacteria, viruses, and insects have selective possibilities in their parasitism. Along with polyphagy, particularly among insects, the majority of species of parasitic fungi, bacteria, viruses, and even insects, have become adapted in their evolution to definite genera and species of plants.

Practically, we first distinguish the phenomena of immunity and resistance associated with the *specialization of parasites,* according to genera and species of host plants. There is no sharp limit between varietal, specific, and generic immunity, but nevertheless we can commonly observe that a high degree of resistance to disease in a variety bears a relation to its species or even genus. This is expressed so sharply that immunity may be used as one of the methods for determining the relationships of plants.[41]

The most widely distributed forms of immunity among plants are *generic and specific immunity.* Whole genera and species are resistant to certain diseases. In approaching the problem of selection or the creation of resistant forms, the breeder first of all must know the degree of specialization of the parasite, *i.e.,* the species and genera of plants entering into the cycle of its adaptation, and also the specific differentiation of the host plant. An incompatibility of a parasite with a given species or genus of plant ordinarily takes the form of a sharply-expressed immunity, usually an entirely indifferent relationship between parasite and host, and the absence of reactions on the part of the plant cells to injury by the parasite. Recently E. KÖHLER has proposed calling the occurrence of specialization *absolute immunity within the orbit of the given parasite.* On the basis of concrete facts, however, it appears to us that such an absolute point of view is excessive. Practically absolute immunity is frequently found in certain varieties of plants within the limits of a species. For example, we have varieties of Persian wheat, *Triticum persicum* Vav., which are absolutely unaffected by powdery mildew (*Erysiphe graminis*), while the oat variety Mesdag (*Avena sativa*) as well as some varieties of *Avena brevis* and *Avena strigosa,* are almost entirely unaffected by smut.

There has recently been discovered the complicated makeup of parasitic species which we will discuss later, and which has obliterated the limits between specific and varietal susceptibility. Varieties which are resistant to a high degree, as we may see from many examples that have been recently studied, frequently correspond to botanically separate species or particular geographic races of host plants, but on the whole, in practice, specialization of parasites on genera and species of plants is so extensive that it is necessary to divide it into separate basic categories. From this we conclude that *immunity which is associated with biological specialization of parasites on genera and species of plants is dependent on the processes of divergence of host plants and parasites in their evolution.*

Turning to ordinary varietal immunity we first distinguish *active* or *physiological immunity associated with the reactions of the host plant cells* following inoculation with a parasite.[42] In the phenomena of immunity, we must distinguish two phases in the development of parasites, namely *the penetration of the parasite into the plant, and the distribution and development of the parasite*

[41] VAVILOV, N. I.: Immunity to fungus diseases as a physiological test in genetics and systematics, exemplified in cereals. Jour. of Genetics. Vol. 4, 1913. At the present there might be cited hundreds of facts confirming the basic thought in this publication, illustrated by the most diverse plants.

[42] The term "active or physiological immunity in plants" must be sharply distinguished from the conception of active, acquired immunity in animals and man.

within the tissues of the host plant. The relationship between parasite and cells of the host tissues in the second phase is usually very complicated in cases of active immunity and the appearance of so-called humoral reactions, *i.e.*, the production by cell parasite and host of complex chemical compounds, usually of protein character. By analogy with animal immunity, we may speak of the production of toxins by the parasite, and of antitoxins or antibodies by the host cell, these antibodies appearing in the form of lysins, dissolving antigens which act on parasitic fungi, bacteria, or viruses, in the form of agglutinins or clumping antibodies, or in the form of precipitins, precipitating antibodies. In isolated cases the production of such substances has been shown experimentally. Recently NOBÉCOURT has chemically determined the presence in plant sap of antitoxins corresponding to definite fungus toxins, since he showed that the antibodies produced were observed only in the presence of the fungus. Agglutinins were found in infected roots of legumes with bacterial galls, but in general this field of study has been worked over very little, as may be gathered from the foregoing section. Furthermore, as has been seen from the work of NOBÉCOURT, antibodies, or antitoxins for the most part have been determined in plants in relation to saprophytes or hemisaprophytes and least of all in cases of parasitic fungi such as rusts and powdery mildews. DUFRÉNOY tested BESREDKA's local immunity in plants in connection with the relationship between tissues of the chestnut and *Phytophthora cambivora* (1930). In all the literature of this aspect of immunity there is observed a definite tendency to consider the phenomena of plant immunity as analogous with processes occurring in animals, but little proof of this is offered.

The relationship between parasites and host tissues in active immunity is very complicated, and is observed in different degrees: from a practically complete or absolute immunity down to weak resistance. Active immunity may be accompanied not only by physiological and chemical reactions, but sometimes there appear certain anatomical changes, for example, the isolation of fungus hyphae by tissues of the host plant.

NOËL BERNARD (1909) noted in orchids a phenomenon reminding one of phagocytosis in animals. The role of phagocytosis in plants, however, as admitted by all authors (NOBÉCOURT, p. 153), is very limited.

In the early phases of development of parasites, frequently there may be observed a positive chemotropic effect of plant cells on fungus hyphae. The British mycologist, MASSEE (1904), even developed a comprehensive chemotropic theory of immunity, although he noted its inadequacy with broadening knowledge of the subject (see VAVILOV, "Immunity," 1919). The penetration of the parasite through a stoma or through the epidermis is only the beginning phase of parasitism, and such tropisms would not apply to later relationships between the parasite and the cells of the host plant.

The American investigator, ALLEN, has studied the cytological behavior of resistant and susceptible varieties of wheat in relation to stem rust, and found in *immune varieties* the following picture of relationships between fungus and host tissues: *a*) the hyphae of the fungus do not as easily penetrate through the stomata as in susceptible varieties; *b*) coming into contact with the cells of the mesophyll, the hyphae cause a killing of the host cells with immediate effect on the hyphae and a plasmolysis of adjacent tissues; in turn toxic substances produced by the dying host cells kill the hyphae and haustoria of the fungus, while in susceptible varieties the hyphae penetrate without hindrance; *c*) the dying cells, which produce toxic substances, become isolated in their effects from the healthy surrounding tissues, with thick cell walls surrounding the dying portion.

On the whole the cytological picture of the behavior of immune varieties in relation to rusts and powdery mildews appears to reveal an antagonism between fungus and host cell. The invading hyphae and haustoria of the fungus do not attain a normal feeding status and die from starvation. On the other hand, in susceptible varieties it appears that the invaded cells are even stimulated and in early stages are even better provided with nutrient substances. Our proposed scale of immunity (1913, 1919) has been constructed on the conception of this relationship between plant tissues and parasites.

Wellensiek (1927), in studying the behavior of susceptible and resistant varieties of corn with rust, showed that in this case the immunity of the variety is related to an exhaustion of the parasite with observable signs of its starvation.

Not infrequently—for example with infection of different species of rusts or powdery mildews—susceptible varieties at first do not suffer, or suffer only very little; the cells remain well supplied with chlorophyll and give a definite impression of the occurrence of symbiosis, at least in the earlier phases. Köhler has proposed naming this kind of close relationship, a sort of high degree of parasitism, *euphagy*. The parasite to a marked extent does not disrupt the basic functions of the host plant, and even may stimulate the plant cells.

"The parasitism of rusts"—writes Nobécourt—"shows unique features; it is a veritable symbiotic association" (p. 13). This symbiosis, however, eventually has ill effects on the plant. The symbiosis commonly appears in susceptible varieties; immune varieties on the other hand, show a sharp reaction to the penetration of the parasite: cells surrounded by hyphae of the parasites quickly die, and with this the fungus dies. In other words, immunity in these cases appears to be the result of a high sensitivity of the tissues to injury by the parasite. Various species of parasitic fungi show a great diversity in the picture of relationships with the tissues and cells of the host plant. For example, in certain smut fungi the mycelium, on infection, grows down as a pollen tube, and with the development of the seed there follows, step by step, the development of the fungus. In the cases of rusts and powdery mildews, the fungus parasite guides its hyphae and haustoria into the intercellular spaces, and in case of susceptible varieties, the cells of the host plant and the haustoria live for some time in a symbiotic state. In a third category of cases, as in cabbage clubroot or wart of potatoes, the parasite penetrates entirely into cells of the host plant and develops at first as a photoplasmic mass, also showing in early phases a symbiotic relationship. In more primitive cases, the fungus penetrates into the living cells of the host plant, kills them by its poisonous secretions, and feeds at the cells' expense. This, for example, is the behavior of *Sclerotinia, Rhizoctonia solani,* and *Phytophthora infestans.* Other types of interrelationships might be noted (see E. Köhler).

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The next *major categories of resistance are based on features of the structure of plants in a morphological and anatomical sense. In these cases resistance of the tissues themselves to injury by the parasite appears to be not active but passive.* In our monograph on immunity we have called this category of resistance *mechanical* or *passive* immunity. It would be more correct to call this *structural* immunity, in a broad sense, associated with resistance based on different morphological and anatomical features of the variety, since these structures arise with no relation to injury caused by the parasite; in other words, this kind of immunity actually appears to be *passive.*

This category may be subdivided according to the factors responsible for resistance. They are as follows:

1. Features of the structure of the epidermis, cuticle, cortex, wax covering the stems and leaves, features of the stomata and lenticels.

2. Features of the blossoms; closed versus open blossoms have decisive significance, for example, in infection by ergot and smuts in cereals. Cleistogamy protects plants from blossom infections.[43]

3. Hulled and naked seed.

4. Features of tissue growth. For example, the rapidity of growth of tissues has significance in the resistance of cereals against infection by smuts and *Fusarium.*

5. The possibility of rapid healing of wounds.

6. The production on the surfaces of cells of slimy or resinous substances or waxy layers, and ethereal oils which protect against penetration by the parasite.

7. The general habit of the plant which may affect its injury by diseases. For example, upright or compact growth; flat or twisted leaves; and hairiness of the leaves and stems, or the absence of such hairiness.

The types of resistance based on structural peculiarities constitute a main division of immunology. A number of authors (*e.g.,* ED. FISCHER, GÄUMANN, and others) propose an entire category of resistance, associated with structural features, and sharply distinguished from real physiological immunity, which is associated with active reactions of the host cells. The investigator of gall formation due to attack by insects, FRITZ ZWEIGELT, proposes calling resistance which is based on structural peculiarities, "pseudo-immunity" (1931). *There is no sharp distinction between active and passive immunity.* Immunity in the early stages of attack by parasites on tissues is often due to structural features of the surfaces of leaves and stems, the structure of the cuticle, stomata, and cortex. Active physiological immunity, the reaction of cells in producing one or another type of compound—"antitoxins"—begins after the penetration of the parasite into the tissues or cells, *i.e.,* passive and active immunity appear in different phases of development of the parasitic relationship.

Varietal differences in relation to attack by insects are quite frequently due to structural features of the plant. Examples of structural immunity may be found in the resistance of protected varieties of sunflowers to the sunflower moth, or the susceptibility of eligulate varieties of cereals to attack by the spring fly, the larvae of which enter freely into the leaf sheath if there is no ligula preventing ingress into the leaf sheath (N. L. SAKHAROV).

In some plants, as a result of attack by insects, there is formed a protective sclerenchyma layer of cells which prevents further spread of the parasite. This appears frequently, for example, in attack of oak by gall-forming cynipids (KOSTOFF and KENDALL, 1929).

In relation to saw flies, resistance of cereals is dependent on structure of the straw. Varieties with solid straw are more resistant than those with hollow straw (SHCHEGOLEV).

In cases of attack by insects, for example the frit fly (*Oscinella frit*), there are good possibilities for the regeneration of the plant after attack, associated with the energy of growth (N. V. KURVUMOV, A. V. ZNAMENSKII, and others).

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The next extensive category of phenomena of immunity in plants is associated with the *chemical properties* of tissues, high osmotic pressure of the cell sap, presence in the cell sap of organic acids, tannins, phenols, and other toxic substances. This kind of immunity we may call *chemical* and at the same time

[43] A number of varieties of barley, for example the group *erectum,* are very little affected by *Ustilago nuda,* since many of these have cleistogamous flowers, forming seed within the protection of the leaf sheath.

it appears to be *passive*. The chemistry of the cells in these cases is expressed through its effect on the parasites.

COOK and TAUBENHAUS have observed the strong effects of *tannic substances* particularly in relation to parasitic fungi. In various cases the role of tannins may be quite significant. This does not yet have general application to other cases, according to recent investigations. BAVENDAMM (1928) has determined, for example, for a number of fungi attacking woody plants, such as *Stereum, Lenzites, Trametes, Polyporus, Merulius,* and *Coniophora,* that they can tolerate tannic substances very well and even use them as food. VALLEAU did not find any connection between content of tannins and resistance to *Sclerotinia cinerea* in plums.

Anthocyanin pigments have often been shown as contributing to resistance to diseases (*cf.* VAVILOV, "Immunity," 1919), but in the literature may be found a considerable number of contradictory facts.

A similar role is played by *osmotic pressure* of the cell sap (*cf.* VAVILOV, "Immunity," 1919), or the presence in cell sap of different organic acids, anthocyanins, and flavones. Direct observations have shown that positive findings of this sort for certain plants and diseases cannot be applied generally to other plants nor to other diseases.

ROBERT NEWTON in Canada and his associates have made a particularly careful study of the chemistry of eight standard varieties of wheat which differ strikingly in reaction to rusts. In addition to the chemical properties they have investigated the electro-conductivity, osmotic pressure, and bound water of the materials. As a result they found that the greatest correlation with immunity was with the quantity of phenolic compounds. Thus, the highly immune variety, Khapli, Indian emmer, showed the greatest amount of phenolic compounds in expressed leaf sap. Next came *durum* wheat (Kubanka), and the least phenols of all were found in common wheats.

NEWTON himself, however, declares at the end of his work that we cannot at present distinguish individual phenols; in expressed sap of plants there are contained different substances, and at present the determination of the phenolic compounds is comparatively crude; "hence it is impossible to draw many significant conclusions from this, but they stimulate and force us to go on" (*cf.* NEWTON and ANDERSON, p. 11, 1929). It is sometimes possible by chemical means, to distinguish immune from susceptible varieties or species. Even crude analyses of seeds and leaves may show striking variations, as in determining the acidity by simple titration (*cf.* VAVILOV, "Immunity," 1919), which has sometimes brought out sharp differences. NELSON and DWORAK (1926), using serological reactions, have found that varieties of flax which are resistant to *Fusarium* belong to one well-marked serological group, which indicates corresponding differences in the proteins. LINK and SHARP (1927) have found that a number of types of bacteria attacking plants show definite serological specificity corresponding to their biological reactions (specialization).

Numerous investigations have been carried out in recent years in studying *the acidity of cell sap* of different varieties in connection with their different reactions to diseases. While at first the method of titrating with alkali was used in studying the chemical composition of attacked and non-attacked varieties, in the more recent investigations the active acidity has been determined more exactly in terms of definite hydrogen ion concentrations (*p*H). Such methods have been applied to many varieties by a number of investigators. Both the method of titration and determination of *p*H have shown the complexity of the relationship between immunity and acidity. In some cases and in some plants, such as grapes, a correlation between immunity and quantity

of acid is comparatively clear, although not absolute; in wheat such a relationship between acidity and immunity has not been observed in relation to rusts, smuts, or powdery mildew.

HURD has investigated the *p*H in cell sap of wheat varieties in relation to stem rust and smuts, and has not been able to determine any definite correlation between immunity and *p*H value. The *p*H values were not found to be significantly different even in the most strikingly distinct varieties of wheat, which acted entirely differently with regard to stem, leaf, and stripe rusts, and also to powdery mildew, species of smut (*Urocystis tritici, Tilletia tritici*), *Gibberella saubinetii,* and nematodes (*Tylenchus tritici*). WEISS and HARVEY did not find such a correlation with respect to resistance of potatoes to wart (*Synchytrium endobioticum*).

W. F. HANNA (1931) in Canada did not find notable differences in oxidase activity in immune and affected varieties of wheat in relation to rust.

In the investigations of A. A. RIKHTER in Saratov there was found a correlation between high peroxidase activity in the roots of sunflowers and attack by broomrape. His student, K. T. SUKHORUKOV, found that forms of composites, *Artemisia* and *Xanthium,* which were immune from broomrape, and also from rust, were characterized by a low peroxidase activity. No other enzymes were found to have a noteworthy role in immunity.

Alkaloids contained in plant tissues, evidently do not always have a protective role. NOBÉCOURT found that atropine, quinine, and nicotine had no effect on *Botrytis cinerea.* It is the opposite with resistance to insects; the chemical composition of the tissues and in particular the content of alkaloids, in this case, plays an essential role.

E. ROKHLINA demonstrated a correlation between resistance of crucifers to clubroot (*Plasmodiophora brassicae*) and differences in the content of *glucosides,* which in fermentation with myrosin give mustard oil. Among such glucosides are singrin, which is found in many species of crucifers (*Brassica nigra, Cochlearia officinalis* and others), gluconasturtin in *Barbarea praecox* and *Nasturtium officinale,* and glucotropeolin in *Lepidium sativum.*

DICKSON, ECKERSON, and LINK found that resistance of wheat seedlings to the fungus *Gibberella saubinetii* was explained by the quantity of pectic substances in the cell walls. The fungus easily penetrates walls which consist of pectin, and is prevented from doing so by walls lacking pectin substances.[44]

REYNOLDS found a correlation between the resistance of flax to *Fusarium lini* and the concentration of the glucoside linamarin in the tissues of different varieties. This glucoside in hydrolysis produces cyanic acid. Extracts of the leaves and stems of flax containing linamarin are toxic to *Fusarium lini.* The quantity of the glucoside varies markedly and is evidently higher in resistant varieties. As a particular case one cannot deny this correlation, but it is hardly possible to apply it to *all varieties of flax* and even less so to other plants.

With respect to the many studies on the chemistry of immune and susceptible varieties of wheat, ROBERT NEWTON writes: "Thus far the investigations have only touched the problem, and only scratched the soil on which slowly, and with great difficulty, will be established the basis of our knowledge" (p. 8, 1929).

On the whole, the phenomena of structural and chemical passive immunity graphically reveal the multiplicity of kinds of resistance and the impossibility of bringing them all into a single system.

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[44] **See Phytopathology, Vol. 14, 1924.**

Hurt (1929) has distinguished, besides physiological and morphological factors of resistance, *"functional resistance."* Some varieties of wheat are resistant in the field during the period of growth, thanks to the particular behavior of their stomata. These varieties can show susceptibility to stem rust in the seedling stage. The rhythm of daily stomatal movement differs with the varieties. In some varieties they are open all day and in others only for a very short time. The critical period for infection by stem rust is early morning, not long before sunrise, when the plants are well covered with dew. If the stomata are open at this period the fungus can penetrate into the tissues; if, on the other hand, they are closed at this time, infection does not occur. Further investigation has shown that this phenomenon is somewhat more complicated. In the mandarin orange the stomata are so constructed that they will not permit the entry of water or bacteria; from this results the resistance of the variety to citrus canker. If the epidermis is removed, the bacteria penetrate and infect the variety (McLean).

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A distinct type of resistance is that of grapes to *Phylloxera*. The so-called "resistant" varieties of grapes, for example different species of American vines, when attacked by *Phylloxera* do not form galls on the roots; the European vines do form galls in the crevices of which there develop bacteria which cause a rotting of the roots. This bacterial disease really appears to be the cause of the damage to European grapes when attacked by *Phylloxera*. The insect in this case seems to be only a contributing factor. Practically, this type of phenomenon, despite its complexity, may be referred to the category of immunity, since the real problem is one of creating varieties that are resistant to infectious disease.

In the phenomenon of gall formation there are observed processes which remind one to a considerable extent of reactions in active immunity. However, Zweigelt (1931), who studied in detail the process of gall formation by aphids, has considered that the immunity in this case is not fully analogous to immunity from parasitic fungi.

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In a final, special category, but not directly related to immunity, is *the escape of plants from infection due to their earliness of ripening before the maximum development of an epidemic.* In this case the varieties which escape attack do not have any real immunity. Early-ripening varieties of cereals, for example oats, succeed in heading before the extensive development of thrips and other insects. Early varieties of barley frequently escape rust, etc. Practically, such varieties are sometimes called resistant, or even immune, in the agronomic literature.

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In concluding this survey of the nature of immunity, there should be noted also *the occurrence of different degrees of resistance.*

In some cases the cause of immunity may be definitely associated with specific factors such as acidity, anatomic structure, etc., but on the whole, so far as present knowledge goes, the nature of immunity is more complicated. Immunity may be regarded as the result of interaction of many components. The immune reactions of cells must be considered in relation to the environmental medium. The investigations of Jones and Dickson in the United States (Madison) and Gassner in Germany, are particularly instructive in this respect. From this we naturally turn to the complexity of the interrelationships of immunity and environment, from which we cannot separate either plant or

parasite, and which must be considered in work on breeding for immunity. The limits between the categories of physiological, structural, and chemical immunity frequently can be defined only with difficulty or not at all. Lines of demarcation between different kinds of immunity often do not exist. We must regard the categories of immunity as being abstract to some extent, embracing diverse phenomena.

4. **Differentiation of Species of Parasites into Physiologic Races:—** Among the great achievements in the past 15 years in phytopathology having direct relationship to immunity, we need first of all to consider differentiation in our conception of parasites. At the end of the 19th century ERIKSSON had determined the presence of biologic races in cereal rusts. These were distinguished not by morphological characters, but only by their adaptation to definite species of plants. Thus stem rust (*Puccinia graminis*) was broken up into the forms *tritici, secalis, hordei,* etc.).

The investigations of E. C. STAKMAN, M. N. LEVINE, and later a large group of American and German phytopathologists during the last two decades, have shown that within these biological species of cereal rusts are to be found many physiologic races distinguished by their infectivity on different host varieties. Old mycological species have been broken up into a great number of races which are morphologically indistinguishable, but are differentiated according to their virulence on different plant varieties. If we take a number of standard, distinct varieties of wheat and infect them with different collections of rust, we distinguish various races of the fungus according to degree of virulence. In stem rust of wheat alone (*Puccinia graminis* f. *tritici*) have been determined more than 150 physiologic races distributed in different territories.

For leaf rust of wheat, in 1934 there had been determined 54 races, including 38 races in the States of North America, 15 in Europe, and 1 in Australia. In stripe rust of wheat there have been found 17 races (see GASSNER and STRAIB, 1934); in bunt of wheat, about 8 races of *Tilletia tritici,* and 4 of *Tilletia levis* (REED); in *Ustilago hordei,* 12 races (RODENHISER); in *Ustilago jensenii,* 7 races; in *Helminthosporium gramineum,* 4 races (RÖMER); in *Helminthosporium sativum,* 37 races (CHRISTENSEN); in loose smut of wheat (*Ustilago tritici*), 14 races (RODENHISER); in smut of oats (*Ustilago avenae*), about 20 races; in *Ustilago levis,* 5 races (RODENHISER); in *Colletotrichum lindemuthianum* attacking beans, 34 races; and in *Fusarium lycopersici,* 24 races (WHITE, 1927). With respect to the number of races within the limits of different species of parasites, we also see a kind of specialization: some of the parasites are less differentiated, others more. For example, thus far no physiologic races have been found in potato wart, *Synchytrium endobioticum.* Up to 1932 there were not known to be races of the potato late blight fungus, *Phytophthora infestans,* despite special investigations in Germany (MÜLLER) and in America (REDDICK). In very recent times, however, in this case there have been found races distinguished on different species, varieties, and hybrids of potato, according to their degree of susceptibility (*cf.* SCHICK, 1932, and MÜLLER, 1933).

In the future the number of races within species of parasitic fungi will undoubtedly be increased.

The different races of parasites are also distinguished by localization of infection. Thus some races of oats smut (*Ustilago avenae*) according to our observations, affect only the stamens. E. E. GESHELE found in Ukraine a race of barley smut (*Ustilago jensenii*) which infected the blossoms.

For determining physiologic races, the pathologist has constructed varietal

keys which have been particularly well worked out for wheat and oats in the United States of America, Canada, Germany, Sweden, and Rumania, according to which the races of parasites may be differentiated. Races in the majority of cases are characterized by definite geographic areas, and not infrequently are very limited in range. No doubt the number of physiologic races of parasites is much greater than has been determined up to the present, particularly if we take into account the fact that in America, where the races of fungi have been studied in particular detail, grain has been cultivated no more than 300 years; wheat, barley, oats, and rye, have been brought there from Europe. We might expect that under the conditions of our region, near to the source of origin of the cereals and of their parasites, the number of physiologic forms of fungi would be still greater. This is indicated, for example, by the finding in Central Asia of new species or biologic races of *Ustilago vavilovii* Jacz, on rye, which were unknown in other regions, an unusual form of *Puccinia graminis,* producing aecia resembling those of cedar rust (*Gymnosporangium*) (*cf.* VAVILOV, "Immunity," 1919), and a different form of *Tilletia,* distinguished by the color of its spores (SPANGENBERGER).

Preliminary experiments by A. A. YACHEVSKI have shown that some of our northern races of wheat bunt, *Tilletia tritici,* are evidently more virulent than American ones. L. F. RUSAKOV noted in 1924 in the Central Chernozem region (Kamennoi Steppe) a massive infection of rye with crown rust, *Puccinia coronifera* Kleb., which usually affects oats, and while this may be associated with peculiar conditions of the season, it also may indicate a particularly virulent race of this fungus distributed in this area.

Interesting investigations of BODENHEIMER (1925) have shown that usually in the native home of given species of host plants, a number of insects which parasitize these species are particularly specialized, much more so than in regions where these plants have been introduced in recent years. This was particularly striking, for example, in Palestine, where BODENHEIMER carried out investigations on Australian eucalyptus, acacia, and casuarina, and on citrus fruits; the native home of the latter is in China and India. Citrus fruits as well as eucalyptus, casuarina, and acacia in Palestine were almost free from injurious insects, although these plants have many such in their native countries.

Differentiation into physiologic races occurs not only in ascomycetes and basidiomycetes, but also in a number of species of imperfect fungi. More and more there is being found a differentiation of virus diseases on various species and genera of plants. Biologic races have been determined also in insects, for example *Phylloxera* and the frit fly. Races of fungi are distinguished primarily according to the species and varieties of host plants which they affect. Differences appear in the degree of virulence in relation to one or more of these varieties.

GÄUMANN found in *Peronospora parasitica* 67 different forms which he distinguished not only by their ability to infect different species of plants, but also according to small quantitative characters, such as the size of conidia. Such forms, which have biological and minor morphological differences, are called *morphological-biological species.*

Sometimes physiologic races of fungi differ chemically, particularly in the character of growth under the conditions of an artificial environment for the parasites, which is found in artificial culture. Such have been found, for example, in different races of corn smut (*Ustilago zeae*), *Fusarium* wilt of flax (*F. lini*), and *Helminthosporium sativum* (CHRISTENSEN). The temperature optima for different physiologic races and in general their relationship to en-

vironmental factors may be different, as has been demonstrated experimentally for leaf and stem rusts and for *Helminthosporium sativum.* Specialized races are usually designated by numbers or letters. As has been shown directly by experiments, physiological differences of rust races appear to be completely hereditary.

Unfortunately the Soviet phytopathologists have barely touched the subject of differentiation of parasites; in this respect the workers in foreign countries have done significantly more.

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The investigations of physiologic races have shown that some of them are very widely distributed, while others have narrowly restricted geographic ranges. For example, STAKMAN and LEVINE have distinguished a race of wheat stem rust which has wide distribution in the United States, Canada, England, France, Norway, Egypt, and even Japan; all of the methods of investigation which could be used indicated that this was actually one and the same race. In other cases, even in different localities of one region, there are encountered different physiologic races. For example, certain varieties of Indian two-grained emmer (variety Khapli) were resistant to 40 different races of wheat stem rust; however, when there was obtained an additional race of stem rust from Egypt, this variety became infected. All of the 40 physiologic races tested infected the soft wheat variety Little Joss, which was developed in England. The Egyptian race of stem rust infected Abyssinian emmer, but showed a lack of adaptation to Little Joss wheat, only infecting it to a weak degree.

The races of stem rust of oats in U. S. A. and in Europe are very different. Moreover, the race constitution of rust may vary from year to year due to the effect of natural selection, and also to the possibility of transport of races from one geographic region to another.

The geographic races of *Tilletia tritici* in England differ markedly in their virulence from those in the United States. In the experiments of GAINES, American resistant varieties planted in England became more strongly attacked than in their native home, and on the other hand, the English varieties showed a higher degree of infection in America.

The introduction of new varieties may evoke marked differences in the race specialization of parasites. Thus, in Germany in 1910 there was introduced into culture the Swedish variety of winter wheat, Svalöfs Panzer, which was practically immune from stripe rust. For a number of years this variety remained unaffected, and it became widely distributed in Germany. In 1923 there was general surprise when it showed a high degree of attack by stripe rust. RÖMER explained this as follows: the physiologic races of stripe rust attacking the variety Panzer had previously either been absent or strictly limited in their distribution. The wider distribution of the variety made possible the wider distribution of physiologic races of its parasite, producing, in 1923, a genuine epidemic.

RÖMER has given another illustration of the distribution of physiologic races in the case of loose smut of wheat (*Ustilago tritici*). In recent years in Germany the spring wheat variety Peragis has become widely distributed. Before this time, on the variety Grüne Dame there was known to be a rare specialized race of loose smut. With the wider distribution of the variety Peragis this race of smut became widely distributed since it showed virulence for this variety, just as for "Grüne Dame."

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KÖHLER has recently reported that the large number of physiologic races which have been determined in recent phytopathological investigations may be to some extent reduced. The determination of the number of races depends on properties of the parasite, and on differences in the host variety. The total number of races is determined by the reactions which result from different factors, including the effect on the variety and on the parasite, and, accordingly, in his opinion, the number of physiologic races of fungi probably may be reduced to a much smaller number. This conclusion deserves attention, but in any case the fact of differentiation of races of parasites is indisputable, and the number of races remains considerable.

The Origin of Forms of Parasitic Fungi.—Very important discoveries recently have made contribution to our understanding of the dynamics of the origin of the forms of parasites in connection with the determination of sexual processes and heterothallism in rusts, smuts, and powdery mildews. As early as 1904, BLAKESLEE, using fungi of the *Mucorales* showed that the mycelium formed from a single spore does not produce zygotes. These result only on the meeting of two mycelia, and then not in all cases but only when the two mycelia, which may be identical in appearance, differ from one another sexually. At the place of contact of two different mycelia there are formed sexual organs, and zygotes result from the conjugation of the male and female gametes. Recent investigations have shown the wide occurrence of heterothallism in many genera of smuts, basidiomycetes. In 1927 the Canadian mycologist, CRAIGIE, demonstrated it for cereal rusts—*Puccinia graminis* and *P. helianthi*. ALLEN (1931, 1932) proved the existence of heterothallism in leaf rust of wheat (*Puccinia triticina*) and in flax rust (*Melampsora lini*); it was also found in *Phytophthora omnivora* (LEONIAN). Heterothallism probably exists in *Puccinia coronata* (CRAIGIE). It should be explained that, as a result of the occurrence of sexual processes, not infrequently there is a crossing of different races of rusts and smuts.

The investigations of CRAIGIE and his school in Canada, who have worked experimentally on the question of hybridization in fungi, have shown that as a result of crossing of stem rust on barberry there are produced various new forms of the parasite, some with greater and some with less virulence in comparison with the parental forms used. Thus, to a certain extent, we can understand the production of new races of parasites. In eastern Canada and in British Columbia, where there are many barberry bushes, this is correlated with the finding of a greater number of physiologic forms of stem rust of wheat than in the plains of western Canada where there is practically no barberry (M. NEWTON). Heterothallism has been demonstrated in *Tilletia tritici* and *T. levis*. Experiments on hybridization of these have been carried out (FLOR, 1932).

DODGE in the New York Botanical Garden has demonstrated the possibility of crossing different species of fungi (*Neurospora*), but it is easier to obtain crosses between different races and varieties of a single species.

Work on rust in the Winnipeg laboratories has shown that the biological species of stem rust, *Puccinia graminis tritici*, may be crossed with *P. graminis secalis*, and that this is followed by a normal process of segregation. Unsuccessful attempts were made to cross stem rust of wheat with species of stem rust occurring on more distantly related genera, such as *Agrostis*.

As a result of these discoveries, mycologists have been able to study the genetics of parasites and the inheritance of both morphological and physiological characters, including differences in specialization on host varieties. In this work it has been shown that inheritance in rusts and smuts follows the Men-

delian law, just as in higher plants. The genetics of the parasites has thus given us an understanding of the origin of forms and the production of new races of parasites.

Direct observations on fungus cultures have brought out the occurrence of mutations and saltations:[45] in smuts there have been found unique recessive forms lacking color, in rusts light and brown colored forms, and also there have been found mutations in rusts, smuts, and *Helminthosporium sativum,* with production of new races distinguished by their various forms (STAKMAN, LEVINE, COTTER, and MITRA).

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The discovery of these facts still further complicates work on immunity. The breeder finds that he must have to do not only with species, but also with races of parasites, and for different regions he must determine the racial constitution of the parasites. The possibility of the origin of new races by hybridization must be considered. Many physiologic races may possibly be heterozygous forms with respect to the character of virulence.

Considering the possibility of the new formation of races, breeding for immunity must be a complex work, always faced with the possibility of the appearance of new and more new forms with different degrees of virulence. It might appear that the skepticism of S. G. NAVASHIN is beginning to be confirmed. As we will see below, however, the case is not altogether hopeless.

5. **Environment and Immunity:**— The reactions of immunity or its reverse, susceptibility, are determined by three categories of factors: the heredity of the variety in question, the selectivity or specialization of the species of parasite or its races, and *the environmental conditions.* A change in the environmental conditions may, to greater or less extent, change the immunity reaction. The normal infection of tissues and cells by plant parasites to a significant extent is determined by the environmental conditions.

The reactions of plants to parasites may be changed by the conditions of the soil environment, particularly its acidity (*p*H value), its physical properties, the presence of various salts, the effects of soil and air temperature and moisture, the effect of light, the quantity of carbonic acid contained in the air, and other factors.

The relationship between immunity and environment with respect to certain diseases has been studied in particular detail by JONES in the University of Wisconsin (U.S.A.). Much attention has been given to the role of the environment in the detailed work of A. ZIMMERMANN (1925-1927) on the relationships between parasites and host plants (Centralblatt für Bakteriologie, II Abt.) and also the school of GASSNER who formerly worked in Uruguay, and at present in Germany. A thorough treatment of this question is given by ED. FISCHER and E. GÄUMANN in their book, "Biologie der pflanzenbewohnenden parasitischen Pilze" (1929).

We will begin with the effect of soil conditions on the development of diseases, and on changes in plant reactions.

Soil Reaction (*p*H).—A very marked effect on susceptibility results from the *reaction of the soil* in which the variety is growing, in other words the *p*H *value.*

For example, in the experiments of E. GÄUMANN, varieties of sugar beet that are usually resistant to the fungus *Phoma betae* (Oud.) Rostr. change their

[45] In those cases where there is no sexual reproduction and where there may be heritable mutations or slower modifications there is a tendency to call the latter saltations (STEVENS, 1922).

disease reaction with variation in the nutrient medium, particularly the soil reaction. If the acidity (pH) does not exceed 6.9, all of the tested varieties appeared to be healthy. At pH 7.2 disease appeared to a limited extent; at pH values above 8.0, beet varieties in these soils, which earlier had shown immunity, contracted infection.

In other words, the immunity of the varieties of sugar beets in this case was not a constant quantity, but was to some extent a function of the reaction of the soil or a function of the nutrition of the variety.

The same picture has been observed in comparatively susceptible varieties of sugar beets (of the type Kleinwanzleben). If these are tested under conditions comparable to those with the resistant varieties, the following results are obtained with respect to the same disease: at pH values up to 7.6 the beet roots remain healthy; at higher pH values the disease appears, and at pH 8.1 the roots become totally affected.[46]

These facts show that the heritable characteristics of the variety are displayed only under certain definite conditions. Immunity and susceptibility appear to be phenotypic showing only consequences of hereditary (genotypic) differences in predisposition.

In the experiments of Chupp (1928) it was shown that the development of cabbage clubroot on crucifers is associated with acid soil. The lower the pH of the soil, the higher the susceptibility of the plant. At pH 7.4, the plants were not attacked by clubroot; at pH 5.8, 100% of the experimental plants developed clubroot. Reed and Faris (1924) found the same true for covered smut of oats (*Ustilago levis* [K. et S.] Magn.). Only at a definite acidity (pH between 7.0 and 8.0) in sand cultures with 20% moisture and with soil temperature from 19-20° C., did the oats (varieties Victor and *Avena nuda inermis*) become infected with smut.

Effect of Soil and Air Temperature.—Immunity not infrequently shows a very marked relationship *to soil and air temperature and moisture.*

For example, the fungus *Gibberella saubinetii* (Mont.) Sacc. affects wheat seedlings at 22-27° C. At these same soil temperatures, seedlings of corn are hardly affected; if, however, the temperature is raised 8°, corn becomes strongly infected by the same fungus. Resistance, as Dickson has shown, is dependent on the hydrocarbons and pentosans which differ in the different varieties, and the amounts of which are conditioned to a large extent by temperature. In other words, in this case we have a clear picture of the relationship between the immunity of wheat and corn and the conditions of the environment, in particular the soil temperature.

L. R. Jones and J. G. Gilman have shown that for infection of cabbage with the fungus *Fusarium conglutinans* it is essential to have "a critical temperature of the soil." At temperatures below 17° even susceptible varieties do not become infected with *Fusarium* even though inoculum is present in the soil. In hot summers, even the most resistant forms may become infected. Varieties which are resistant in a cool climate theoretically might become susceptible if they are brought to a warm climate. Practically, however, varieties that were resistant in Wisconsin where the investigations were carried out showed their immunity from New Jersey to Iowa.

The effect of *air temperature* on changes in resistance is well seen in the experiments of Melhus (1911) with crucifers artificially infected with the fungus *Albugo candida.* At ordinary temperatures the infection did not exceed 5-15%, while at 10-12° it reached 95%. Reed showed that tomatoes were also

[46] This experiment is cited from E. Gäumann: Das Problem der Immunität im Pflanzenreich, 1928.

strongly infected by *Phytophthora infestans* at low temperatures; the same is known for grapes in relation to *Plasmopara viticola.*

Susceptibility of wheat to bunt (*Tilletia tritici* and *T. levis* is evidently related to external conditions at the time of sowing infested seed (see REED, 1924, and others). For strong infection with bunt the favorable factor appears to be low temperature. Thus, in the experiments of FARIS, at a soil temperature of 5° C., 69.8% of the plants were infected; at 10°, 64.6% at 15°, 53.8% and 20°, 15.5%, and at 30°, 1.7%, *i.e.,* the optimum for susceptibility lies near 5° C. This temperature favors the coming together of hyphae of the parasite and the host cells since at low temperatures the wheat embryo is in the most susceptible stage for infection by the smut for a longer time. In this connection it is very important to note that this temperature optimum for infection is not uniform for different varieties. For the variety Marquis, for example, the optimum for infection by smut is 10° C., and for the variety Dawson, 5° C.

The wheat variety Hope, obtained by MCFADDEN from crossing emmer and soft wheat, shows differences in susceptibility to bunt in relation to the temperature. If it is sown at the customary time in the spring (South Dakota) it is resistant to three physiologic races of *Tilletia tritici* and two forms of *Tilletia levis.* If it is sown at the usual time for fall sowing, it becomes moderately affected by all five races. Differential sowings at intervals of a week (SMITH, 1932) have shown that this variety appears to be resistant when sown in cold weather with later growth at high temperatures. If Hope wheat is held at prolonged low temperatures, it becomes infected with bunt. Other varieties of soft wheat (for example, Jenkin) react differently, showing susceptibility at both low and high temperatures. In the experiments of GAINES and STANTON, the variety Marquis, if sown in the spring, is highly resistant to bunt (*Tilletia tritici*). If the same variety is sown in the fall, it is comparatively susceptible to this fungus. The same thing has been found for another variety of wheat—Turkey. When sown in the fall it shows comparatively weak resistance, but when sown in the spring, it is entirely unaffected by smut. Increase in the soil temperature lowers the percentage of infection of oats varieties by the smut *Ustilago avenae* (BARTHOLOMEW and JONES, 1923).

In the investigations of GASSNER and STRAIB (1931) the temperature had very strong influence on the infection of wheat by stripe rust (*Puccinia glumarum*). Only a few varieties of wheat in Germany remain immune under these conditions (*cf.* Der Züchter, 1931).

Soil and Air Moisture; Aeration of the Soil.—Moisture of the soil, just as of the *air,* not infrequently is a factor favoring infection and susceptibility. This is particularly clear in relation to such diseases as rusts, powdery mildew, *Phytophthora* of potatoes, mildew of grapes, and smuts. This factor is also highly correlated with temperature.

For example, it has been definitely noted that ergot in wheat, which is very limited under ordinary conditions, appears in the form of epidemics (up to 10% of the plants affected) when there is high humidity of the air and alternating heat and cold, factors which influence the opening of the wheat blossom.

The moisture of the soil is particularly important in predisposing plants to diseases of roots, tubers, and fleshy roots.

An abundance of soil moisture, along with high temperatures, inhibits the development of oats smut (*Ustilago avenae*) and, conversely, low soil moisture within the limits of ordinary temperatures, is accompanied by a high percentage of infection of oats varieties by this smut (BARTHOLOMEW and JONES, 1923).

TAPKE (1931) showed that for the infection of wheat and barley by loose smut (*Ustilago tritici* and *U. nuda*) it is necessary to have a definite degree of

air humidity. At low air humidies the loose smut develops very weakly. On the other hand, varieties which are almost entirely resistant show as high as 91 or 96% infection with high moisture. The wheat variety Little Club, after infection with smut, was held for eight days at low moisture (11-30%) and at high moisture (58-85%). As a result, the plants in the first group showed 21.9% infection, and those in the second group 94% infection with smut.

ALBERT HOWARD (1921) directed attention to the important role of aeration of the soil with reference to different fungus diseases in India, and to the resistance of varieties with different types of root systems. The relationship appeared to be particularly striking in dealing with hemisaprophytes.

The Role of Light.—The influence of light is definitely related to the display of susceptibility to parasitic diseases. STAKMAN, PIEMEISEL, and LEVINE (1917, 1919) have found that stem rust of wheat does not develop on etiolated plants.

The same was observed by MAINS (1917) in experiments with crown rust of oats. Darkness lengthens the incubation period; light shortens it. If the plants are kept in the darkness, and as a result there is a reduced conversion of carbon dioxide into carbohydrates, these plants become immune from infection by rust. This relationship to carbohydrates has been demonstrated by MAINS in corn leaves deprived of carbohydrates by holding them in darkness. If etiolated leaves are placed in sugar solutions, they become susceptible to development of *Puccinia sorghi.* With an insufficient quantity of CO_2 in the air, which prevents the normal accumulation of carbohydrates in the leaves, this rust does not develop.

GASSNER and APPEL (1927) have shown that with supplementary night lighting of wheat and oats (2000 candlepower) the number of pustules of rust (*Puccinia triticina* and *P. coronifera*) increased four fold. The same thing has been demonstrated for stem rust of wheat (GASSNER and STRAIB, 1928).

Although in relation to rusts the question of the influence of light is comparatively clear, with respect to other parasites the effect of this factor has not been well explained and the data are contradictory. In contrast to rust, seedlings of wheat were infected by the fungus *Gibberella* more strongly in the presence of reduced light (DICKSON, ECKERSON, and LINK, 1923); THOMAS (1921) found that etiolated celery (*Apium graveolens*) is less affected by *Septoria apii* Rostr. than normally green celery.

The effect of light under the conditions of nature is interwoven with that of other factors such as warmth and moisture of the soil and air. The effect of one factor may be annulled by that of other factors.

Fertilization.—We, as well as STAKMAN and AAMODT, were unable to increase susceptibility of wheat to rust in the field by strong nitrate fertilization. The same thing was noted by HENNING and other authors. On the other hand, SPINKS and PANTANELLI obtained positive results from nitrogen fertilization of wheat and beans in the sense of increasing susceptibility to rust (*Puccinia glumarum* and *Uromyces fabae*). The same thing relates to the role of potassium fertilization. MÜLLER, MOLZ, SPINKS, SCHAFFNIT and RUMP observed increased resistance to *Puccinia glumarum, P. graminis,* and *Uromyces pisi* as a result of adding potassium salts to soil. In other cases this was not observed. BIFFEN, WEISS, and others were unable to note any effect of phosphoric acid salts on the susceptibility of cereals to rust. GASSNER found that fertilization of cereals with phosphates decreased their rust infection. This he explained as being due to the fact that the fertilized plants, at the time of the development of the rust epidemic, had attained a stage at which *Puccinia graminis* was no longer dangerous to them. From his experiments (1916) it is clear that a

shifting of the stage of development of the plant when the parasite appears may result in an alteration of the relationship between plant and rust. It is evident that the simple formula often encountered and indicating the strong positive effect of nitrogen salts in increasing susceptibility, and of increasing resistance by adding salts of P_2O_5 and K, applies only in exceptional cases. For example, in relation to bunt of wheat and flax rust, nitrogen fertilization reduces infection and strong fertilization with phosphorus salts increases infection by the fungi (HART, 1926, BURK, 1923). But in all cases it is impossible to ignore entirely the role of fertilization in the expression of susceptibility of varieties to infectious diseases.

Salts of lithium increase resistance of wheat to powdery mildew (see SPINKS, VAVILOV, 1919). According to R. CASPAR (1926) calcium nitrate reduces infection of wheat by bunt. In many cases in using different kinds of fertilizer, one can note a definite effect on increasing or decreasing immunity.

In recent years, very important studies along this line have been carried out by the school of GASSNER in Germany.

GASSNER and HASSEBRAUK have found that K and P salts strikingly change the susceptibility of wheat varieties to leaf rust. Nitrogenous compounds whether inorganic or organic (asparagin, glycocol, urea) increase susceptibility. This effect of nitrogenous substances is observed under conditions in which the plants have an adequate supply of carbon dioxide.

Contradictory results of different authors are commonly due to different methods of evaluating infection. A number of authors who have reported a favorable effect of nitrogen have failed to take into account the increase in the surface of plant organs available for infection. The conditions of the environment, the soil reaction, the stage of development of the plant, all have great significance on the expression of the effects of fertilization.

The effects of fertilization differ with different parasites and in relation to other factors of the environment and to host varieties.

Parasites and Hemisaprophytes.—In many investigations the authors have come to the conclusion that between the parasitic fungi (such as rusts and powdery mildews) and the hemisaprophytic ones (such as *Gibberella saubinetii* or different species of *Fusarium* and *Botrytis*) there are definite differences in relationships to the host plant. The latter group develop particularly well on weakened plants, the former on normally developing plants. This explains to some extent the differences in degree of attack by one or another parasite under different environmental conditions. Susceptibility to hemisaprophytes is particularly influenced by changes in different factors of the external environment. If we create favorable conditions for the growth of the plant, at the same time we reduce the effect of hemisaprophytes, and in contrast, we may be increasing the opportunity for infection of the varieties by typical parasitic fungi.

The known facts indicate that the thing which is inherited is not a definite degree of immunity or susceptibility, but a norm of reaction under different conditions. *Changes in the environmental conditions may change immunity.*

The Effect of Environment on Physiologic Races of Parasitic Fungi.—The differentiation of species of parasites has led to a revision of older views, particularly with reference to the relationships between environment and immunity.

It might naturally be expected that different physiologic races of a fungus might react differently to external conditions. The experiments of GASSNER and SCHNEIDER show clearly the differences in the reactions of parasitic races with respect to temperature. Thus, a number of varieties of wheat tested for infection by German races of leaf rust behaved as resistant at a temperature of

20° C., while if the temperature was lowered to 6° C., and with a lengthening of incubation up to one month, these varieties became susceptible. At the same time, GASSNER and SCHNEIDER found a number of very resistant varieties of wheat, such as *Triticum monococcum,* and the varieties Bezeler and Dickkopf, which showed no change in resistance when the temperature was varied. The varieties that were more resistant in the field were also resistant under various environmental conditions in the greenhouse.

With stripe rust the reverse was true. It was found that the resistance of varieties was increased as the temperature was lowered. JOHNSTON has shown that the effects of different temperatures may change the reaction of wheat varieties toward certain physiologic forms of stem rust. At low temperatures the varieties show immunity, while at higher ones they become susceptible. Light may also change the reaction of varieties toward certain physiologic races of rust. Given influences of light and warmth within definite ranges apply only to certain varieties of wheat in their reaction toward certain physiologic races of parasites. The same variety does not change its reactions to other races of rust under the influence of warmth and light.

The Relation of Growth and Stages of Development to Susceptibility.— Growth and the growth stage of the plant have no less significance for the expression of immunity reactions. STAKMAN and PIEMEISEL (1917) have shown that strains of orchard grass are comparatively uniform in susceptibility to stem rust at different stages of development. In species of *Agropyrum* and *Elymus* they found a lowering of susceptibility with advanced growth. Timothy and *Agrostis alba* on the other hand, showed more resistance to stem rust in earlier stages of development. In other words, we can distinguish diseases of early stages of growth and diseases of more mature plants. Different organs of plants show different degrees of susceptibility. For example, with dahlias inoculated with *Bacillus felsineus,* the tuberous roots become severely diseased, while at the same time the stems do not react at all to the infection (CARBONE). Powdery mildew (*Erysiphe graminis*) attacks seedlings of cereals only very lightly.

Vernalization of cereals evidently favors infection by smuts in some varieties of wheat and oats, and it may be that this effect is not only on the host tissues, but also on the smut fungus itself. For example in the spring sowing of 1933 in Detski Village, many varieties of vernalized oats and wheat showed much more development of smut (*Ustilago avenae* and *U. tritici*) than control, non-vernalized plants.

According to the observations of M. VEIDEMAN at the Institute of Plant Industry, vernalization alters the time of ripening and this may favor or impede the optimum development of stem and leaf rust and may, in different varieties, either increase or decrease resistance.

Vernalization evidently favors the escape of tomatoes from infection of virus diseases (RIZHKOV and KARACHEVSKII, 1934).

Oats which are infected with smut are evidently more strongly attacked by rust than non-smutted oats. (*cf.* WELSH, J. N., 1931).

A comparison of the experimental data on the effects of different environmental conditions shows the great role that environmental factors play in shifting immunity. At the same time the experimental data show a great stability of immunity in those cases where we are dealing with one disease, with one given physiologic race, *and under ordinary conditions of field culture.* In many experiments with wheat and oats using different fertilizers the heritable differences of the plants with respect to rust immunity appear to be very con-

stant. The immunity is frequently retained even under the most diverse conditions.

During the period 1923-1934 we conducted geographic tests to study the behavior of given wheat varieties toward leaf and stripe rusts in different regions of Russia. As a rule, the common European durum wheat, *Triticum monococcum,* emmers, *T. persicum,* and *T. timopheevi* everywhere showed resistance to both rusts.

In recent years we have studied the behavior of certain varieties and species of cereals in different regions of Asia and North Africa, and North and South America. It was seen that differences in the race constitution of the parasite and in the environment resulted in corresponding differences in the behavior of a given variety. Nevertheless, in those cases where it was possible to determine exactly the species and varieties, we usually observed a striking conservation of immunity under the most varied conditions. For example, in 1932, we studied the stripe rust and stem rust reactions of a collection of wheats from the Experiment Station in Lima, Peru, under optimal conditions for infection: with irrigation and artificial fog. In spite of this, the behavior of the species and varieties of wheat with respect to stripe rust, was the same as had been determined for other regions. The same thing was determined in Argentina where the conditions for infection of wheat with stripe and stem rust are particularly favorable. Durum wheats, as well as a number of European emmers, did not become infected with stripe rust.

Argentine oil flax is entirely resistant to *Fusarium, Polyspora,* and anthracnose. In North Caucasus, Leningrad, and other regions of SSSR, these varieties retained their resistance.

The Persian wheat (*Triticum persicum*) which we found in 1913, is almost totally resistant to powdery mildew and shows this resistance in Japan, England, the United States, and Canada, under both field and greenhouse conditions. Only in Georgia (Russia) and Armenia, the native home of the species *T. persicum,* are there races of powdery mildew which somewhat (weakly) infect certain forms of this wheat species.

Varieties and species of wheat which are quite distinct in their immunity from different species of rust in our country show approximately the same behavior in Canada, as we ascertained in 1932. The same may be noted also for the United States. All durum wheat varieties such as Kubanka, Garnovka, Acme, Pentad, and Monad, according to the observations of STAKMAN, MARTIN, and CLARK, are noteworthy in America as well as in Russia for their immunity from stem rust. The same may be said of emmers (Khapli, Vernal).

The varieties of common wheat, Webster, Hope, Marquis, Kota, Kanred, Cooperatorka, and the emmers, Vernal and Khapli, show identical resistance to stripe rust under field conditions in North America and in Argentina (RUDORF, 1933).

In the experiments of REED and FARIS, varieties of sorghum that are immune from smuts (*Sphacelotheca sorghi, S. cruenta*) show their resistance under different conditions of culture with respect to temperature (from 12° to 37.5° C.) and moisture (from 10 to 80%). REED, GRIFFITHS, and BRIGGS, in New York, have conducted extensive investigations on the resistance of species and varieties of oats to smut. There, variety and species reactions fully agreed with ours, determined independently in Moscow. The same thing may be seen in the experiments of K. VON ROSENSTIEL (1929) in Germany. Our characterizations of numerous species of cultivated and wild oats, including particular varieties, such as Mesdag, Burt, Red Rustproof, and Fulghum, have been fully confirmed by the data of VON ROSENSTIEL.

In comparing the data of GAUDINEAU (1932) in France on the behavior of species and varieties of wheat and also *Aegilops ventricosa* and *A. triuncialis* with our data on smut, *Tilletia tritici,* one cannot help but note the similarity in behavior of given varieties in Russia and in France.

Varieties of roses react identically toward powdery mildew (*Sphaerotheca pannosa* Lév.) and rust (*Phragmidium subcorticinum* Winter) in different regions.

Direct testing has shown that there are many varieties which show immunity from complexes of different races of rusts, smuts, and powdery mildews under the most diverse conditions of the Old and New World.

The variety of apple, Northern Spy, shows identical resistance to red rot in Australia, in England, and in other European areas.

On the other hand, we must not overlook the importance of cases of the reverse type of behavior. Thus, the coffee tree (*Coffea arabica*) in Java is strongly attacked by rust, *Hemileia vastatrix,* at altitudes of 1300-1500 meters. Above 1500 meters the coffee tree appears to be resistant (ED. FISCHER and E. GÄUMANN, *l.c.*). The appearance of new physiologic races of fungi in different regions, finally, may result in corresponding changes in the reactions of varieties. The behavior of varieties in the greenhouse, as we will see below, frequently is quite different with respect to rusts, powdery mildew, and other diseases, from their behavior in the field.

In the monograph on plant immunity (1919) we reported a large number of experiments which we conducted in studying the influence of environment on changes in immunity from rust and powdery mildew, and came to the conclusion that immunity from a given parasite, from the point of view of breeding, is comparatively constant. Geographic plantings in the most widely separated regions of SSSR and abroad, experiments testing the effects of different combinations of fertilizers and specific substances, and experimental data on the conservation of reactions for immunity in the components of so-called graft-hybrids (*cf.* the work of ED. FISCHER and G. SAHLI), all testify to the constancy of varietal reactions toward different parasitic fungi, which very much facilitates the breeding and introduction into culture of immune varieties.

The role of environment as seen in the foregoing discussion, however, cannot be entirely by-passed in the question of immunity, even though, for practical purposes, marked differences in immunity act as comparatively constant, particularly when there is an expression of immunity from many physiologic races of a parasite at one time. Nevertheless, we must always be prepared for the possibility of its changing under the influence of certain environmental factors, and we must make efforts at increasing immunity. In approaching the task of developing and creating immune varieties, the breeder must know the specific particulars of the etiology of the parasite, using this knowledge to guide his breeding work; he must know the specific relationship between parasite and plant and select those forms which are most resistant and least variable in this.

Virus Diseases of Plants.—Many viruses appear to be almost omnivorous, attacking plants of different families without relation to their phylogeny. The ringspot virus attacks genera belonging to eleven different families. Cucumber mosaic attacks eleven genera. In this respect viruses remind one of the effects of hormones and enzymes.

External conditions appear to have unusually marked effect on the development of virus diseases. Immune species of tobacco become susceptible at high temperatures. Even the persistence of viruses in a given host plant varies. JOHNSON has found that tobacco viruses will affect potatoes, although viruses

from potatoes would not affect tobacco. SCHAFFNIT has shown that a tobacco virus which will not directly affect potatoes may do so if the virus is first passed through tomatoes. As has been shown by direct experiments, some viruses may be passed through immune tissues without losing their activity.

Nevertheless, within the limits of species of some plants there have been found marked varietal differences in reaction to various viruses. Thus, there are a number of varieties of beans which are resistant to bean mosaic and to curly top. Bean varieties such as Corbett Refugee, Great Northern U. I. No. 1, Robust, and Wisconsin Hybrid Wax No. 536 show resistance to virus 1 (see work of W. H. PIERCE, 1934). The amplitude of host ranges of different viruses affecting legumes differs strikingly. For example, the number of genera of hosts affected by alfalfa virus 2 is much greater than with bean viruses 1 and 2 (PIERCE, 1934). Certain varieties of cucumbers are resistant to cucumber mosaic. The resistance of sugar cane to virus has been most thoroughly investigated.

In studying the resistance to viruses, we must consider their dissemination, and the necessity for the presence of certain insects, for example, aphids, which transmit viruses.

6. **Genetics of Immunity:**— During the past decade, a large number of works have been devoted to the genetics of immunity. In the recent Japanese review of genetics by MATSUURA (2nd edition, 1933), there is given a review of all important investigations on genetics of plant immunity up to 1929. A particularly valuable critical review of present knowledge on the inheritance of immunity is that of the Danish investigator HANSEN (1934) in which there is given a very complete bibliography on the genetics of immunity through 1932.

Unusually detailed investigations have been made of the immunity of wheat in relation to rusts and smuts. Literally hundreds of publications have been devoted to this. These studies outnumber all other works on the genetics of immunity in plants. A considerable number of studies have been made on the immunity of oats, corn, potatoes, flax, barley, cotton, beans, tobacco, grapes, and onions.

A fundamental principle in crossing immune and susceptible varieties is the application of MENDEL's Law.

The first investigators of the inheritance of immunity determined the facts of segregation in the crossing of resistant and susceptible forms, the possibility of combining immunity with other characters of susceptible varieties, and demonstrated the transmission of immunity in simple, monohybrid ratios. Such was the study of BIFFEN (1905), who first showed that immunity of wheat from rust follows MENDEL's Law.

Not infrequently in these first works, the authors simplified the phenomena, schematized the numerical relationships, and to some extent interpreted more complicated relationships by simple, monohybrid formulas, 1:3, or 1:2:1.

In such simple schemes there were even included the numerical relationships obtained in crossing distantly related forms, such as species of wheat with different numbers of chromosomes, without giving consideration to the fact that here the process of segregation results in sterility, the non-existence of many combinations, and the lack of viability of many gametes and zygotes, and consequently the small probability of simple relationships in immunity.

For example, BIFFEN, in crossing common and English (*T. turgidum*) wheats, determined two factors conditioning susceptibility to ergot, but did not consider sterility. In such crosses some of the progeny have open, sterile blossoms, and it is these which become infected with ergot. As shown in our

investigations (VAVILOV, "Immunity," 1919), there are no specific genes for immunity in this case, but rather the occurrence of sterile plants with blossoms which are open as is customary for sterile blossoms of cereals, and it is these blossoms which, to a considerable extent become infected with ergot. Further and more thorough investigations have disclosed more complicated relationships. Monohybrid segregation does occur, but it is comparatively rare.

Comparing the data in the literature, HANSEN has given us a list of established *monohybrid* combinations. This is given below as it refers to the most thoroughly studied species.

PLANTS:—	PATHOGENS:—	AUTHORS:—
Oats	*Puccinia coronata*	DAVIES, JONES, DIETZ, MURPHY
Oats	*Puccinia graminis avenae*	DIETZ, GARBER, GRIFFEE, HAYES, STEVENSON, LUNDEN, WATERHOUSE, WELSH
Oats	*Ustilago avenae*	BARNEY, GARBER, GIDDINGS and HOOVER, REED, VON ROSENSTIEL
Oats	*Ustilago levis*	COFFMAN, STANTON, BAYLES, WIEBE, SMITH, TAPKE, GARBER, GIDDINGS, HOOVER, REED
Cabbage	*Fusarium conglutinans*	WALKER, WELLMAN
Barley	*Helminthosporium californicum*	MACKIE
Barley	*Puccinia anomala (simplex)*	WATERHOUSE
Barley	*Rynchosporium secalis*	MACKIE
Barley	*Ustilago nuda*	NAHMMACHER, ZEINER
Barley	*Erysiphe graminis hordei*	BIFFEN, DIETZ, MURPHY
Lettuce	*Bremia lactucae*	JAGGER
Flax	*Melampsora lini*	HENRY
Rice	*Helminthosporium oryzae*	NAGAI, HARA
Beans	*Colletotrichum lindemuthianum*	BURKHOLDER, MCROSTIE, SCHREIBER
Timothy	*Puccinia graminis phleipratensis*	BARKER, HAYES
Peas	*Fusarium orthoceras* v. *pisi*	WADE
Potato	*Synchytrium endobioticum*	SALAMAN, LESLEY
Wheat	*Puccinia glumarum*	ARMSTRONG, ISENBECK
Wheat	*Puccinia graminis tritici*	AAMODT, GOULDEN, NEATBY, WELSH, HARRINGTON, HAYES, STAKMAN, MELCHERS, PARKER, QUISENBERRY, WATERHOUSE
Wheat	*Puccinia triticina*	ISENBECK, MAINS, LEIGHTY, WATERHOUSE, JOHNSTON
Wheat	*Tilletia tritici*	BRIGGS, CHURCHWARD
Wheat	*Ustilago tritici*	PIEKENBROCK
Wheat	*Septoria tritici*	MACKIE
Corn	*Puccinia sorghi*	MAINS
Sorghum	*Sphacelotheca sorghi*	SWANSON, PARKER

In the great majority of the cases given, immunity is clearly dominant.

Dihybrid inheritance has been shown for oats with respect to crown and stem rust and smut (*Ustilago avenae*), in flax in relation to rust, in beans in relation to *Colletotrichum lindemuthianum, Fusarium martii phaseoli,* and mosaic, in potatoes in relation to wart, and in wheat in relation to leaf and stem rust and also bunt (*Tilletia tritici*).

The ratios observed in dihybrid crosses were—9:3:3:1; 15:1; 9:7; 3:13; 12:3:1.

There is only one case of a conclusively determined *trihybrid* ratio, namely in experiments in crossing beans resistant to *Colletotrichum* with susceptible varieties (SCHREIBER, 1933), where there was observed a ratio of 27 resistant plants to 37 susceptible ones.

Polymeric ratios, without an exactly determined number of factors, have been found in the following plants with respect to the given diseases (according to HANSEN).

PLANTS :—	PATHOGENS :—	AUTHORS :—
Oats	*Puccinia coronata*	PARKER
Oats	*Puccinia graminis avenae*	DIETZ
Oats	*Ustilago avenae*	BARNEY, GARBER, GIDDINGS, HOOVER, HAYES, GRIFFEE, STEVENSON, LUNDEN, NICOLAISEN, REED, WAKABAYASHI
Oats	*Ustilago levis*	COFFMAN, STANTON, BAYLES, WIEBE, SMITH, TAPKE, GAINES, GARBER, HOOVER, WELSH, and others
Cabbage	*Fusarium conglutinans*	WALKER
Cantaloupe	*Erysiphe cichoracearum*	JAGGER, SCOTT
Cotton	*Fusarium vasinfectum*	FAHMY
Barley	*Helminthosporium gramineum*	ISENBECK
Barley	*Helminthosporium sativum*	GRIFFEE, HAYES, STAKMAN, CHRISTENSEN
Barley	*Ustilago nuda*	NAHMMACHER, ZEINER
Flax	*Fusarium lini*	BURNHAM, TISDALE
Tobacco	*Thielavia basicola*	JOHNSON
Beans	*Colletotrichum lindemuthianum*	TEN DOORNKAAT KOOLMAN, REDDICK, HAMMARLUND
Beans	*Fusarium martii phaseoli*	BURKHOLDER
Peas	*Erysiphe communis*	HAMMARLUND
Pea	*Ascochyta pisi*	HAMMARLUND
Currant (genus *Ribes*)	*Sphaerotheca mors-uvae*	LORENS
Rye	*Puccinia dispersa*	MAINS, LEIGHTY
Potatoes	*Phytophthora infestans*	MULLER, NILSSON
Potatoes	*Synchytrium endobioticum*	MULLER, ORTON, SALAMAN, LESLEY, SNELL, WEISS
Wheat	*Erysiphe graminis tritici*	VAVILOV
Wheat	*Fusarium* sp.	CHRISTENSEN, STAKMAN
Wheat	*Puccinia glumarum*	ISENBECK, NILSSON-EHLE, PESOLA, RUDORF
Wheat	*Puccinia graminis tritici*	CLARK, AUSEMUS, SMITH, HARRINGTON, HAYES, AAMODT, STEVENSON, MCFADDEN, NEATBY, GOULDEN, QUISENBERRY, STEWART, WALDRON
Wheat	*Puccinia triticina*	MAINS, LEIGHTY, and JOHNSTON
Wheat	*Tilletia tritici*	AAMODT, GAINES, GIESEKE, KNORR
Grapes	*Plasmopara viticola*	SEELIGER
Corn	*Gibberella saubinetii*	HOPPE, MCINDOE
Corn	*Ustilago zeae*	JONES

In the majority of cases of the inheritance of immunity that have been studied by hybridization and where there is an exhibition of polymerism, there has usually been observed some transgression or the appearance, in the hybrid progeny, of plants which are more resistant or more susceptible than the respective parental forms. The exact number of genes determining immunity or susceptibility in cases of polymeric inheritance cannot be determined without involved study. For this it is necessary to study in detail the F_3 and F_4 generations under conditions of maximal artificial infection, which may be a difficult undertaking.

A classic example of a genetic study on immunity is given in the work of NILSSON-EHLE with stripe rust of wheat (1911), which was carried out under field conditions.

The German breeder RÖMER (1933), whose school in recent years has done much in studying the specialization of parasitic fungi and in breeding for resistance, has given us the following record of the genetics of immunity from important diseases of cereals.

DISEASES :—	IMMUNITY :—	AUTHORS :—
Bunt—*Tilletia tritici*	Recessive, polymeric	KNORR
Loose smut—*Ustilago nuda tritici*	Recessive, monomeric	PIEKENBROCK, GREVEL
Barley smut—*Ustilago nuda hordei*	Dominant, monomeric	ZEINER
Oat smut—*Ustilago avenae*	Dominant, monomeric	VON ROSENSTIEL
Oat smut—*Ustilago avenae*	Dominant, monomeric, dimeric and trimeric	NICOLAISEN
Helminthosporium gramineum	Dominant, polymeric	ISENBECK
Stripe rust, *Puccinia glumarum*, on winter wheat	Dominant, mono- and polymeric	HUBERT, ISENBECK
Stripe rust, *Puccinia glumarum*, on spring wheat	Recessive, monomeric	ISENBECK
Leaf rust, *Puccinia triticina*	Dominant, monomeric	ISENBECK

Some authors distinguish, along with basic genes which determine immunity and susceptibility, *modifying* genes, which strengthen or weaken immunity, but actually these genes are difficult to distinguish from basic genes in cases of polymerism.

Very probably there are not only *independent genes* for immunity giving simple, arithmetical results when their effects are combined, as occurs in classic cases with such polymeric characters as color of grain (NILSSON-EHLE), but also *dependent genes,* the interactive effects of which give a more complicated result that is distinct from a simple addition of effects. Recent investigations in genetics, particularly with physiological characters, such as the vegetative period, have forced us farther and farther away from schemes of polymerism, to the consideration of dependent genes and their mutual effects in the appearance of external characters.

The investigations of HAYES and others have shown that different genes simultaneously determine immunity from a number of physiologic races of *Puccinia graminis tritici, P. graminis avenae,* and *P. sorghi.* SCHREIBER (1933) found that resistance of the bean variety "Anthracnose Resistant Pea 22" is not affected by 34 races of *Colletotrichum lindemuthianum,* and that this is determined by 8 genes. In other words, many of these genes are characterized by *pleotropic* effects.

There is no question of the possibility of combining immunity with other varietal characters using hybridization within the limits of a species. Recently breeders have created a number of valuable immune varieties by crossing. We note the outstanding works of Argentine breeders in creating varieties resistant to stripe rust and the works of English, Swedish, and German breeders, particularly on wheat. All of these accomplishments definitely show the possibility of hybridizing to create new combinations which unite immunity from rust and from other diseases.

Cases of linkage and established genetic correlations between immunity and other morphological and physiological characters are comparatively rare. The most striking example appears to be the correlation of red and yellow color in the outer scales of onions and resistance to *Colletotrichum circinans.* In the outer colored scales there are found phenolic compounds including protocatechuic acid, which is soluble in water. RIEMAN found by infection experiments with hybrid onions that there is a close relationship between their resistance to *Colletotrichum circinans* and the scale pigment, when shows that the pigmentation and resistance are determined by one and the same gene. The same thing is seen in sweet corn where the gene for sweetness has a positive effect on the resistance of the hybrid. The sugar creates an environment for the development of parasites.

As regards *dominance and recessiveness* for immunity we find that the

situation varies with the plant variety and the disease. Sometimes immunity is recessive, and sometimes it is dominant. Of 26 experiments in crossing wheat for resistance to rusts and smut, including intra- and inter-specific combinations, MATSUURA's review (1933) gives 15 cases in which immunity was dominant, and 11 in which it was recessive. *In cases of sharply expressed physiological immunity, in crosses with susceptible varieties, immunity is usually observed to behave as dominant.*

Thus, in the work of WAKABAYASHI, when the Mediterranean oat *Avena byzantina* (*sterilis*) was crossed with *Avena orientalis* (34% infected) in the first and second filial generations there was no smut (*Ustilago avenae*). In the F_3, 94 lines were free from smut when artificially inoculated, and 12 lines were attacked. WAKABAYASHI (1921) came to the conclusion that there are three dominant genes for smut resistance in *Avena sterilis*. GAINES observed the same thing with respect to *Ustilago levis* and the same species of oats (three dominant genes). Identical behavior was observed in different varietal combinations. In the experiments of REED (1925) the variety Mesdag, which is highly resistant to smut (*Ustilago avenae*) and has black glumes, was crossed with the susceptible *Avena nuda* var. *inermis*. In the second generation there were obtained 25.6% infected plants. The third and fourth generations confirmed the dominance of immunity. Resistance to crown rust was also dominant in the most diverse varietal combinations of *Avena byzantina* (Burt X Sixty Day, etc.) in the experiments of PARKER and others.

In the work of RUDORF, the varieties of soft Chinese wheats (166, 165) which are strongly resistant to stripe rust, showed a dominance of resistance over susceptibility in crosses. In our own experiments, crosses of the Persian wheat, which has almost absolute resistance to powdery mildew, with different susceptible species showed that immunity was always dominant.

The character of strong resistance to *Aphis* is dominant in crosses of varieties of plums (BEACH and MANEY). The susceptible varieties Montmorency and Wyant, when crossed with resistant sand cherries, gave resistant progeny. The strongly-expressed resistance to *Phylloxera* in grapes, in the experiments of RASMUSON, showed itself to be dominant in crosses.

MAINS, LEIGHTY, and JOHNSTON crossed two varieties of wheat, Fulcaster and Kanred, of which the first is resistant to race 9 of leaf rust, while the second is susceptible. The second generation, as well as the first, showed dominance *differing in relation to the phase of plant development*. In the seedling stage susceptibility was dominant over immunity with a 3:1 ratio. In later phases, the heterozygous plants changed their reaction and showed more resistance. Homozygous plants, whether resistant or susceptible, conserved their reaction throughout all phases of growth.

The investigations of HAYES, AAMODT (1923, 1925), GOULDEN (1929), and QUISENBERRY (1930) have shown clearly that it is impossible to draw conclusions on the behavior of plants under field conditions from studying hybrid wheat seedlings in the greenhouse with artificial rust infection. GOULDEN, NEATBY, and WELSH (1928, 1931) found that although hybrids of the wheat H-44-24 X Marquis segregated in the seedling phase in the greenhouse as typically dihybrid with respect to physiologic races 21 and 31 of *Puccinia graminis tritici*, in the field these hybrids showed a monohybrid segregation.

In general, the works of American investigators (United States and Canada) show a high degree of rust susceptibility in seedlings. GASSNER, in Uruguay, came to the opposite conclusion, finding that resistance to *Puccinia graminis* and *P. coronifera* in wheat, barley, and oats became less with advanced age of the host plant. This contradiction is explained by the fact that

GASSNER's observations were exclusively in the field; the other authors compared the behavior of seedlings in the greenhouse with the behavior of older plants in the field, where as we know, resistance of cereals increases with higher temperatures.

HONECKER (1934) has shown that dominance and recessiveness of immunity from powdery mildew are associated with the conditions of infection. For example, at 15-25° C. and in diffuse light, young barley plants behave as though immunity was recessive. On the other hand at 25-35°, with intense direct light, susceptibility appeared to be recessive and immunity dominant. Hence, in genetic studies of immunity one must consider the conditions of infection, and it is not always reliable to compare experiments involving infection of young plants in the greenhouse with the behavior of older plants in the field.

Practically, it is very important to note that one can not always reach conclusions as to the behavior of varieties in the field from knowledge of their behavior in the greenhouse.

Differences in growth may be accompanied by different reactions toward narrowly specialized parasites. This is seen in relation to stem rust of wheat and oats.

Crosses Between Distantly Related Species.—In crossing different species which are distantly related to one another and show differences in chromosome numbers, segregation is usually complicated, which is associated with an absence of conjugation of parts of chromosomes, the appearance of sterility, the non-existence of many combinations, the lack of viability of gametes or zygotes, and the large numbers of genes which are different in the species.

Although it is very difficult to obtain desired combinations in crosses of distantly related plants, nevertheless, as shown by direct experimentation, this has been accomplished in a number of experiments. MCFADDEN in South Dakota obtained the valuable varieties Hope and H-44-24 by crossing *Triticum vulgare* × *T. dicoccum*. The hybrids were resistant to smut and rust. HAYES produced the rust-resistant variety Marquillo by crossing *T. durum* × *T. vulgare*, and GOULDEN obtained interesting forms by crossing Marquis (*T. vulgare*) with Pentad (*T. durum*). Similar hybrids have been obtained by us in Saratov, Odessa, and in Kinele (KONSTANTINOV, P. N.).

The process of segregation in such hybrids is quite complicated. In the hybrid progeny correlation between resistance to rust and a number of morphological characters has been observed in the case of *T. durum* × *T. dicoccum*. HAYES, PARKER, and KURTZWEIL have noted that in their crosses of *Triticum vulgare* with *T. durum* and *T. dicoccum*, in the F_3 out of a total of 20,000 individuals lacking this combination there were found a few which combined immunity with the head type of *T. vulgare*.

A number of investigators (SAX, TOCHINAI and KIHARA) have shown a connection between the number of chromosomes and immunity, in crossing species of wheat with different chromosome numbers. Nevertheless, this association is not absolute, as SAX, KIHARA, and THOMPSON first assumed, but relative. THOMPSON and STEVENSON found among the progenies of such interspecific hybrids, forms with 42 chromosomes, resembling *T. durum*, but susceptible, as are the common wheats. The same conclusion was reached by workers in the Breeding-Genetics Institute in Odessa (A. A. and L. A. SAPEHIN and GESHELE) and J. B. HARRINGTON in Canada, working with extensive materials.

This is confirmed by the fact that the Abyssinian hard wheat, which has the same number of chromosomes as the Mediterranean wheat and our com-

mon varieties of this species, is distinguished from the latter by its comparative susceptibility to leaf rust. K. O. MÜLLER (1928), in crossing resistant and susceptible species of potatoes, did not find that susceptibility to *Phytophthora* was dissociated from such characters as productiveness, earliness, color of tuber, etc. In the experiments of ED. FISCHER with hybrids of species of the mountain ash, *Sorbus aucuparia* and *S. aria,* of which the first is resistant to rust (*Gymnosporangium tremelloides*) while the second is susceptible, immunity was not found to be associated with any particular leaf form. In the F_2 segregation, the leaf form varied from the simple, undissected form of *S. aria,* to the more complicated pinnate structure of *S. aucuparia.* Either susceptibility or immunity was associated with both types of leaves.

In comparing immunity with other characters of the parental species, *T. vulgare* and *T. durum* or *T. dicoccum,* one often notes that there are variations from the usual numerical ratios in segregation, which evidently are associated with abnormalities in conjugation of the chromosomes.

Means of establishing fertility in hybrids between distantly related parents, such as occurs with amphidiploids as in tobacco (KOSTOV, EGIZ, and others), in hybrids of cabbage and radish (KARPECHENKO), and in *Brassica napocampestris* from crosses of *B. napus* and *B. campestris* (FRANDSEN and WINGE, 1932), theoretically opens up the possibility of more and more distant crosses for the purpose of creating new forms.

Vegetative reproduction gives us the possibility of a wider utilization of distant hybrids in fruit and berry crops, potatoes, and sugar cane.

In this connection the work of BREMER in Java on sugar cane (1928) has particular interest. He crossed the cultivated cane, *Saccharum officinarum,* with the wild cane *S. spontaneum,* the latter being resistant to two virus diseases of this plant, the mosaic disease "Gelestrepenziekte" and "Sereh," which resembles leaf curl in potatoes. These species of cane easily produced fertile hybrids, although *S. officinarum* has 40 chromosomes (haploid number) and *S. spontaneum* has 56. In the F_1, the number of chromosomes was 136 (2N) instead of the expected 96, which was associated with a doubling of the chromosomes in the 40-chromosome maternal parent, either at the time of fertilization or in the zygote directly after fertilization. This doubling of chromosomes often takes place in *S. officinarum* when it is crossed with distantly related species. Meanwhile, a doubling of the chromosomes in the sperm nucleus did not occur. The first generation of hybrids of *S. officinarum* $\times$ *S. spontaneum* with 136 chromosomes was distinguished by immunity from both diseases. In the reduction division of the F_1 hybrids, the sexual cells had about 68 chromosomes (half of 136), but with some variation in the number, due to incomplete conjugation. These 68 chromosomes included 40 from *S. officinarum* and 28 from *S. spontaneum.*

In back-crossing the F_1 with *S. officinarum,* there were obtained forms with 148 chromosomes, of which 120 originally came from *S. officinarum,* and 28 from *S. spontaneum.* Also in this case the plants, after back-crossing, were immune from both diseases, but their sugar content, as in the F_1, was still insufficient (less than in the original cultivated parent).

Continuing the improvement, plants that were obtained as a result of the first back-cross were again crossed with *S. officinarum.* There were obtained plants having approximately 114 chromosomes, of which 100 came from *S. officinarum* and only 14 from *S. spontaneum.*

The plants obtained were very resistant to mosaic and entirely immune from the "Sereh" disease. They were very rich in sugar content, sometimes

even exceeding the cultivated parent in this respect. These plants were reproduced vegetatively.

In this way was obtained the immune variety P.O.J. 2878, which exceeds in sugar content all of the old Chinese cultivated varieties of sugar cane. In 1922 it was propagated vegetatively, and in 1928 this variety occupied some 60% of the total sugar cane acreage in Java.

When Bremer carried out the reverse cross in the 4th step of the process, he obtained susceptible plants. In other words, by an appropriate combination of chromosomes with the aid of back-crossing, there was solved the important practical problem of creating highly productive and immune varieties of sugar cane, a problem which was comparable to that now facing European and American growers of sugar beets.

The immune hybrids have been obtained by introducing new genes from immune species. In this, the doubling of chromosomes has not changed immunity, at least in a number of cases. For examples Klebahn found that tetraploid tomatoes (*Solanum lycopersicum gigas*) were just as susceptible to *Septoria lycopersici* as the ordinary tomato.

For breeding there is great importance *in combining at one time and in a single variety immunity from several diseases.* Many isolated species of plants are distinguished by combined immunity from several diseases and from large numbers of physiologic races of parasites. The question whether immunity in these cases depends on the pleotropic effect of a single gene or on several genes, must be determined by future investigations.

In any case, the distribution of immunity shows many examples of this kind of combination. Genetically, in a number of studies, it has been shown possible to combine immunity against several diseases in a single variety.

Reed and Welsh found that resistance to *Ustilago avenae* and *U. levis* in certain varieties, for example in Mesdag, is due to a single gene or to closely associated genes. In other cases, for example in crossing *Avena sativa* × *Avena byzantina* (Early Gothland × Monarch), the genes for resistance to these species of fungi were unrelated.

In many varieties of *Avena byzantina,* as well as in *A. brevis* and *A. strigosa,* resistance to smut is coupled with resistance to crown rust, and by crossing the first of these species with *Avena sativa,* it has been possible to obtain varieties that are resistant to both diseases.

The coupling of immunity from stripe and leaf rusts has been shown in wheat (Hayes, Aamodt, and Stevenson, 1927). Waterhouse found in one of his crosses of common wheats an association of immunity from one of the most virulent races of powdery mildew (*Erysiphe graminis tritici*) and immunity from a virulent race of leaf rust (*Puccinia triticina* f. *Australia 1*). Hubert (1932) combined immunity to leaf and stripe rusts in a single wheat variety.

* * * * *

In summarizing this review of genetic investigations, we must emphasize the complexity of the genetics of immunity. It is evident that many of the reported simple Mendelian relationships applied to whole species of parasites need to be reconsidered in view of knowledge of the diversity of physiologic races within the limits of a species of parasitic fungus, which was not formerly considered in the presumed simple relationships. In the light of present day differentiation of parasites, simple ratios of segregation for resistance to complexes of physiologic races of parasites, gives us a schematic result. The presence in nature, within varieties, of large numbers of differential heritable dif-

ferences with respect to susceptibility, again reveals the great number of factors determining immunity.

The presence of many physiologic races of parasites greatly complicates the methods of genetic investigations. In conducting experiments on the genetics of immunity at the present time, the differential study of different races of the parasite is required. Up to now this has largely been limited to *Puccinia graminis tritici,* but no doubt in the work on stripe and leaf rusts of wheat and also with smuts the distinction of physiologic races in refined genetic studies appears to be obligatory (*cf.* NEATBY and others). Finally, in investigations on the genetics of immunity one must consider the environment, since the reactions of plants often have a significant relationship to the conditions of temperature and moisture. Thus, different races of a fungus may react differently toward a single environmental factor, and the numerical relationships in segregation may vary under different environmental conditions. GORDON found, for example, that one of the lines of oats of the variety Juanette showed different relationships to the physiologic races of *Puccinia graminis avenae,* 1, 2, 3, and 5, at low (57.4° F.) and at high temperatures (75.4° F.). At low temperatures this variety was resistant to forms 1, 3, and 4, and heterozygous with respect to form 5; at the higher temperature, it was heterozygous to forms 1 and 3, and susceptible to forms 4 and 5.

7. **The Breeding of Resistant Varieties:**— Despite the inadequate genetic work on immunity of plants, breeding has developed very widely during the past decade. Almost every breeding station today is engaged, on a greater or lesser scale, in breeding for immunity. This work is particularly intensive in United States, Canada, Argentina, Sweden, Germany, and England. Many of the newer varieties of wheat are distinguished by comparative resistance to rust. A number of new American varieties of wheat are resistant to smut. The same may be said for oats varieties. We note extensive work on the hybridization of grape species to obtain so-called "direct-producing" varieties resistant to *Phylloxera* and mildew. Along with ordinary searches for heritable forms, and their use for breeding in the first generation, recently, principally in Germany at the Institute of Professor BAUR in Müncheberg, much attention has been directed to the finding of valuable combinations in the second generation, obtained from extensive hybridization with second generations numbering millions of plants which are infected artificially in the greenhouse, with a culling out of all susceptible plants. The few resistant plants obtained are subjected to further careful study. On a broad scale, analogous work with grapes has been recently carried out by us at the Experiment Station for Grapes in Odessa.

In England there is particular interest in the work of BIFFEN in creating wheats resistant to stripe rust. Of the more interesting American works, we note the investigations at the Minnesota station where at the present time the phytopathologists STAKMAN and LEVINE and the breeder HAYES are working. In Kansas, interesting work on resistance to Hessian fly has been carried out under the direction of PARKER. In Canada there has recently unfolded extensive work on the immunity of wheat at the experiment station in Winnipeg, where the work involves cooperation of phytopathologists, breeders, biochemists, and physiologists.

We note extensive work on breeding potatoes in relation to potato wart, both in Western Europe and in the United States. With respect to *Phytophthora* and viruses there is particularly important work at the Berlin Biological Institute, and in the Netherlands, headed by QUANJER.

In plants that are propagated vegetatively, interspecific hybridization has been widely used, for example in grapes, potatoes, and tree fruits. In plants that are propagated by seed, the most effective practical method has been hybridization within the limits of closely related species or of a single species.

Laws in the Distribution of Immunity from Infectious Diseases in Plants.— In breeding for immunity, it is necessary to consider: *1*) the presence of different physiologic races of the parasite; *2*) the areas of distribution of the different physiologic races; *3*) variety differences in reaction toward the different physiologic races; *4*) the possibility of combining in a single variety resistance to different parasitic races; and *5*) the possibility of producing varieties that are resistant to several diseases. Decisive factors in breeding for immunity appear to be the *individuality of the parasite* against which resistant forms are to be developed, and the *individuality of the original variety.* A basic rule in the distribution of immunity among varieties which we developed in our book, "Immunity" (1919), may be stated as follows:

1. *The weaker the expression of specialization of parasites on genera and species of host plants, the less the chance of the existence of (and consequently of finding) immune varieties.*

If a fungus does not distinguish between generic and specific characteristics of host plants, it is quite improbable that it will differentiate between the comparatively less fundamental morphological and physiological properties of varieties within the limits of a single species in the host range. On the other hand, narrow specialization, limited to one or a few closely related species, is associated with differences in reaction of parasites toward varietal peculiarities. There have been disclosed in recent years, within the limits of specialized species of parasites, a great number of physiologic races of complex interrelationships, but on the whole they conform to the general law. Therefore, where there is specific or even generic specialization of a parasite, we may expect to find immune varieties.[47] Investigations of immune varieties logically should

[47] As an exception to this rule the well-known uredinologist, ARTHUR, refers to the work of C. W. HUNGERFORD and C. E. OWENS ("Specialized varieties of *Puccinia glumarum* and hosts for variety *tritici*," Journal Agr. Res., 25, 363-402, 1923) in which the authors point out that *P. glumarum tritici* attacks 59 host species belonging to the genera *Elymus, Bromus, Phalaris,* and others. At the same time, as is well-known, a great number of varieties of wheat (no less than half) show immunity from this fungus. From this fact, ARTHUR concludes that weak specialization does not exclude the possibility of the existence of immune varieties within the limits of a species (ARTHUR, J. C., "The Plant Rusts," 1929).

In the work by HUNGERFORD and OWENS, in addition to data on artificial inoculation of seedlings of *Phalaris canariensis, Bromus tectorum, Bromus inermis,* and *Elymus australis* with wheat stripe rust, there are given numerous results from field and greenhouse observations on species and varieties of wheat showing marked differences in immunity from stripe rust. In this respect, the results with varieties of common durum, and club wheats, and also emmers and einkorns agree with our data in Russia as well as with observations in Germany, Sweden, France, and Argentina.

The authors' data on the absence of narrow specialization of stripe rust (*Puccinia glumarum tritici*) are contradictory to the exactly determined recent data on the occurrence of narrow specialization of 17 physiologic races of wheat stripe rust (see RÖMER, "Immunitätszüchtung," 1933, and GASSNER, 1934). Further investigations are necessary. It is possible that in part of the experiments of HUNGERFORD and OWENS on specialization, the stripe rust was introduced in seed, which not infrequently can occur, and which even led ERIKSSON to the mycoplasm theory. Stripe rust is no doubt present in many races (as in the case of stem rust) adapted to a wide range of cereals and grasses including *Phalaris* and *Bromus,* and the possibility is not excluded that in the seed with which HUNGERFORD and OWENS worked, there already was infection. We have demonstrated this fact with *Puccinia glumarum* in wheat and *Erysiphe graminis* in *Avena pubescens* under conditions of such isolation in the greenhouse that the fungus could not have been introduced and have produced infection from outside.

be preceded by a study of specialization of the parasite, and this also applies to virus diseases.

2. The second rule is that *the distribution of immunity in narrowly specialized parasites to a great extent is associated with the genetic differentiation of the varieties.* The greater the genetic and physiological differentiation within the limits of a given plant, the more sharply it is divided into species (for example in oats, wheat, and cotton, including the differences in chromosome numbers), the more clearly the species or groups of species are differentiated geographically—the more probable it is that one will find immune forms.

On the other hand, the absence of differentiation of plants into geographically isolated species leads to the small probability of finding sharp contrasts in immune reactions. This rule is confirmed by a great number of facts known for many plants, and essentially resulting from the study of evolution. The evolution of parasites, to a considerable extent, is closely bound to the evolution of the host plants.

Recent data on the differentiation of species of parasites into physiologic races confirm this rule. We can see that disease reactions on the whole correspond with the phylogenetic differentiation of species and geographic groups in wheats, oats, barley, roses, grapes, etc. Isolated races of parasites are more limited in their host ranges of species and varieties than others; they exhibit a greater selectivity of hosts than the less isolated races.[48]

According to the data of S. P. Zibina (Institute of Plant Industry), observations in Leningrad Province (Detski Village), in Voronezh (Steppe Station), and in North Caucasus (Otrada Kubanskaya), and also according to data from artificial inoculations in the greenhouse, the distribution of immunity from fungus diseases in flax varieties shows the following geographical regularity:

	In relation to:—		
	Melampsora lini	*Colletotrichum linicolum*	*Polyspora lini*
1. Mediterranean large-seeded varieties of flax (Algeria, Morocco, Palestine, Tunisia, Cyprus)	Very resistant	Resistant	Moderately resistant
2. Argentine varieties	Very resistant	Resistant	
3. Indian varieties	Very susceptible	Susceptible	Susceptible
4. Abyssinian varieties	Susceptible	Susceptible	Susceptible
5. Central Asiatic (Tadzhikistan, Uzbekistan)	Susceptible	Susceptible	Susceptible
6. Asia Minor (Anatolian)	Susceptible	Susceptible	Susceptible
7. Western China (Kashgariya)	Susceptible	Susceptible	Susceptible
8. Afghanistan	Susceptible	Susceptible	Susceptible
9. Ukrainian area	Moderately resistant	Susceptible	Susceptible
10. European long-fibered varieties	Moderately resistant	Susceptible	Susceptible

On the other hand, from all the experiments including those of Hungerford and Owens, it is apparent that infection of seedlings, under the usual moist conditions of artificial infection in the greenhouse, is stronger than under usual conditions in the field. The variety Hope, according to the observations of Rudorf (1933) in Argentina, is susceptible to stripe rust on artificial inoculation in the seedling stage, while it is very resistant in the field.

[48] See, for example, our work: "Materials on the question of resistance of cereals to parasitic fungi" (Trudy Mosk. Selekts. Stants. 1: 1-108, 1913), where there are given the field characteristics of species, and varieties of wheat in relation to leaf rust, *Puccinia triticina,* and the recent work of C. Calniceanu, "Beiträge zur Resistenzzüchtung gegen *Puccinia triticina*" (Kühn-Archiv, 37, 1933).

These characteristics of the geographic groups are based on tests of several hundred well-distributed specimens, including a full representation of the world's diversity of flax varieties. Entirely distinct, according to immunity, are the Mediterranean large-seeded forms (*macrospermae*) and their derivatives, the Argentine flax varieties. These varieties are genetically separated as a distinct group. Immunity is also widely distributed among the northern long-fibered forms which are extensively grown in the northern European part of SSSR. On the other hand, the Indian, Abyssinian, Central Asiatic (including Afghanistan), and Asia Minor forms are an overwhelming majority of highly susceptible endemic varieties of flax.

Prospects of Breeding for Immunity.—The great assortment of new species and varietal material uncovered in recent investigations of the Institute of Plant Industry for most of the important cultivated plants, provides a new basis for work on immunity. Enormous amounts of new varietal materials of wheat, oats, flax, potatoes, corn, and cotton are available for the indispensable systematic study of the reactions of different varieties, different subvarieties, and geographic groups of varieties, with respect to various parasites. At first the investigations must be directed toward a systematic study of the distribution of immunity in species and varieties and widely separated geographic races of plants in relation to the important diseases.

A basic problem for work on the concrete theories of breeding for immunity is a study of the selection of parental pairs for crossing. A re-studying of the species composition of cultivated plants in recent years has opened up new horizons for immunity breeding. New starting materials are available today to the Soviet breeder, and these must be studied in detail as regards their behavior toward diseases caused by important parasites. This work gives a basis for systematic breeding for immunity.

For example, in breeding potatoes for immunity from *Phytophthora,* an important part must be played by the use of wild Mexican species of potatoes which are resistant to *Phytophthora.* Investigations of S. M. Bukasov have clearly shown that all of the Mexican group of varieties of wild potatoes are distinct from the South American forms in their immunity from *Phytophthora* (*Solanum demissum, S. antipoviczii,* and others).

Among the wheats have been found a number of new species, such as *Triticum timopheevi* and *T. persicum,* which are highly resistant to different diseases. When tested in Georgia (SSSR) *T. timopheevi* showed resistance not only to powdery mildew and rust, but also to *Fusarium* (Dickson).

The group of wheats that are most resistant to different diseases appears to be the group of cultivated species with 28 chromosomes, among which is found a wide range of variation in resistance to different species of rusts, smuts, and powdery mildew (*Triticum durum* subsp. *expansum* Vav.; *T. persicum* Vav.; *T. timopheevi* Zhuk.; a series of geographic races of *T. dicoccum,* which are highly resistant to rust, powdery mildew, and smut). The determination of a large number of new subspecies and species in this group of wheats directs attention first of all to this group, in breeding for immunity. The group of 14-chromosome wheats, although including very resistant forms and even being on the whole characterized by immunity as shown by tests, presents greater practical difficulties in crossing. This is associated with their genetic peculiarities.

Widely separated geographic races, just as species of plants, are sharply distinguished according to their immunity. Whole regions are characterized by varieties that are immune from certain parasites. For example, in European breeding for immunity of tree fruits, particular interest attaches to spe-

cies and varieties of pear, apple, peach, quince, and plum of China and Japan, which are resistant to our diseases. The same might be said for wheats. The durum wheats of Abyssinia are comparatively susceptible to leaf rust. The durum wheats of Europe and the shores of the Mediterranean Sea are distinguished by marked immunity from leaf and stripe rust. Whole geographic groups of flax (Argentina, Morocco) appear to be immune from *Fusarium, Polyspora,* and rust.

Many of our northern races of fiber-flax are also resistant to these diseases.

The study of world diversity of varieties of various plants for the purposes of separating out the forms that are most resistant to different diseases, of determining the laws of distribution of immunity, and of selecting the most valuable parental pairs for crossing—this is the basic, concrete problem of the present time. The great quantity of new varietal and even species materials of cultivated plants, and new introductions of culitvated plants, make the problem a particularly urgent one. This work, despite its importance, has not yet been accomplished.

With plants which are cross-pollinated, such as corn, sunflower, rye, and beet, it is possible to obtain forms that are resistant to narrowly specialized parasites by means of inbreeding, with the isolation of lines that are least affected on artificial inoculation. Thus, a number of American breeders have produced lines of corn that are comparatively resistant to smut (*Ustilago zeae*) by inbreeding. Different lines, as shown by direct experimentation within the limits of a single, inbred variety, are sharply distinguished according to their resistance to smut. By further selection, and crossing such lines with one another, there have been created more resistant varieties (F. R. Immer, 1927).

The experiments of Hayes, Stakman, Griffee, and Christensen have shown (1924) that ordinary varieties of corn are very heterozygous with respect to immunity from smut and that by means of artificial self-pollination there can be derived very resistant lines possessing hereditary differences in immunity. This shows, in their opinion, that the number of genes controlling immunity from smut in corn is comparatively small. Even the localization of smut infections is associated with hereditary differences in the lines. In one form, most of the infection is on the ears; in another, the tassels; in a third, the lower nodes of the stem; and in a fourth, the infection appears over the entire plant.

A second factor in the further work of the breeder is *the necessity of introducing geographical principles into investigations of immunity.* American and German investigators have proceeded by differentiation of parasites and studying their racial constitution in different regions. No doubt we, too, should conduct studies along this line. The significance of geographic races of parasites cannot be underestimated, an example of this being the determination of marked differences in geographic races of the sunflower broomrape, in Kuban and the region of the Lower Volga. The Kuban race known as "malignant broomrape" attacks all of the resistant varieties of sunflowers grown in the Saratov area.

For species of rusts and smuts of cereals it is necessary, without delay, to determine the physiologic races in the basic agricultural regions of SSSR. It is necessary to discover the most widely distributed, the most virulent, and the most dangerous races. At central stations, with all possible precautions, there should be cultured all of the races, as is done in Canada, United States, and Germany, for preliminary testing of newly-developed varieties. It is necessary to have special greenhouses for carrying out experiments on the study of

physiologic races and to resort to artificial infection to determine the possibility of the existence of different physiologic races.[49]

A very instructive example is that of breeding sorghum for resistance to smut—*Sphacelotheca sorghi.* For a long time, varieties of Milo, Hegari, and Feterita were considered immune from this disease, both on artificial inoculation and under ordinary conditions in the field. In 1923, however, this smut was found on Milo in several locations in Kansas, New Mexico, and Texas. In 1924, it was found not only on Milo, but also on Hegari. Experimentally it was determined that this was due to a distinct physiologic race of smut, from which only the variety Feterita was immune. The Milo and Hegari did not lose immunity from this fungus, but there appeared a new race of the smut to which these varieties were susceptible.

In beginning with investigations on physiologic races of parasites, at the same time it is necessary to study the phytogeographic possibilities of our regions and the behavior of assortments of varieties of given plants in a geographic plan.

In the geographic study of the behavior of varieties, or in testing their reactions to geographic complexes of parasitic races (*e.g.,* smuts), we are motivated by the comparatively small extent of investigations on the race constitution of parasites. Phytopathologists have only begun the differential study of parasites. It is the same as with the constitution of our cultivated plants and their close wild relatives, where we are only beginning to discover the species composition, and already, in a short time, there have been found a great number of forms that were recently unknown, species and varieties of wheat, potatoes, and other plants.

Theoretically, it is very probable that the number of physiologic races of parasites is much greater than has been determined up to this time. The closer we get to the sources of origin of species and forms of cultivated plants, and closely related wild species, the more probable it is that we will find new races of parasites corresponding to these. There have been discovered unique forms of *Puccinia graminis* in Persia and West China on barberry (see VAVILOV, "Immunity," 1919), and peculiar forms of smut, *Ustilago,* on rye in the locations of species and variety origin of rye and wheat, and this shows the probability of discovering races of numerous other parasites.

Following the differential study of races and of varieties in relation to them, the investigator, for economy of effort and maximum practical results of breeding, can then proceed to a study of immunity on a wide geographic scale by planting standard varieties, and including, so far as possible, related botanical variants. The planting and the study of relationships to parasites must be carried out under optimal conditions for infection, and in all principal regions of culture of the given plant. In other words, we consider it indispensable to conduct systematic plantings of basic assortments during several years and in different regions, under various conditions, or conducting the experiments by means of artificial inoculation with samples of parasites which have been collected systematically from different locations where the host plant

[49] The best-developed experimental establishments are those in the Winnipeg laboratory for rust study in Canada, at St. Paul in Minnesota under Dr. STAKMAN, and Dr. RÖMER's in Halle, Germany. The greenhouses are divided into compartments for the isolation of different races of fungi. A description of the method of infection and the construction of the greenhouse may be found in the publication by Dr. T. RÖMER, "Immunitätszüchtung" (Flora 28, N. F., 1933), in the reports of the Winnipeg station (*e.g.,* NEWTON, M. and JOHNSON, T.: "Studies in cereal diseases. VIII" Can. Dept. of Agr. Bull. 160, Ottawa, 1932), and in the last chapter of the book by J. C. ARTHUR, "The Plant Rusts." New York, 1929.

exists and might be cultivated. This gives us the possibility, in a short time, of obtaining varietal characteristics in relation to the principal diseases, although at first without exact knowledge of the pathogenic components of geographic complexes of parasites.

A most urgent problem is *to work out the techniques of infecting varieties.* Although this is not necessary in the cases of some diseases where one may use natural infection, growing the varieties under optimal conditions for infection, for many diseases the experimenter must have methods for artificial inoculation which take into consideration the environmental conditions necessary for optimal infection. Many of the investigations carried out in recent times are not conclusive because of an inadequate knowledge of infection techniques.

The procedure of inducing artificial infection for breeding purposes, in some cases may be very useful, particularly for orienting the different varieties as to resistance, but this procedure must be used with care if we are dealing with varietal differences that are not great. We have a very instructive example in the work of HARLAND with cotton. He used a number of varieties of Egyptian cotton. Under conditions of artificial inoculation all of them were infected by bacterial blight (*Bacillus malvacearum*); without artificial inoculation in nature, it was observed that some varieties differed in the degree of rapidity with which the bacterial disease developed. In certain varieties it appeared very early, while in others only at the end of the vegetative period. The experiments showed that by selecting varieties with late development of the disease, and by crossing these, it was possible to create forms which had an even greater degree of resistance, and thus HARLAND produced a resistant form of Sea Island cotton. If he had limited himself to artificial inoculation experiments, these variety differences would have been obscured. In this case he proceeded very carefully in the selection of immune forms, considering the possibility of accumulative breeding for immunity.

For conducting artificial inoculation experiments, as far as possible it is desirable, in the stages of orientation, to use the most virulent races of the parasite.

The greatest attention is necessarily directed toward *group immunity.* During recent times there have accumulated a large number of facts showing that not infrequently single species are resistant to several diseases, *i.e.,* they show group immunity. In the last analysis, the breeder is interested in producing such varieties. In the monograph on "Immunity" (1919) we have presented a large number of facts for cereals and roses showing the occurrence of group immunity toward several diseases. Thus, many species of wheat combine at once resistance to stripe rust, leaf rust, and even stem rust, and also to powdery mildew and to bunt—*Tilletia tritici* (see GAUDINEAU). A number of species of oats are resistant to both leaf rust and smut. Hull-less barley is resistant to both *Helminthosporium gramineum* (ISENBECK, 1930) and *Ustilago nuda* forma sp. *hordei* (NAHMMACHER, 1932). Many varieties and species of roses are resistant to both rust and mildew. American grapes are resistant both to *Phylloxera* and to mildew. E. B. MAINS and M. MARTINI have found a number of varieties of barley (Bolivia, C. I. 1257, Sulu, C. I. 1022, C. I. 1021, and Weider) that are resistant both to different races of leaf rust (*Puccinia anomala* Rostr.) and to powdery mildew (*Erysiphe graminis hordei* Marchal). As shown by the work of the oats section of the Bureau of Plant Industry in Washington (STANTON and others), by crossing *Avena byzantina* with *A. sativa* it is possible to obtain oats varieties which are at once resistant to stem and crown rust, and also to two species of smuts (*Ustilago avenae* and *U. levis*).

Recent works have shown that many varieties of cereals are resistant to dozens of physiologic races of rust; there have even been obtained varieties which are practically resistant to all of the various physiologic races. SCHREIBER in Germany has found beans which combine resistance to 34 different races of *Colletotrichum*. The Kanred variety of winter wheat is resistant to 62 races of *Puccinia graminis tritici*. SCHATTENBERG (1934) has shown experimentally that the oats variety Black Mesdag is resistant to the most diverse geographic populations of smut (from 39 localities). This kind of complex immunity expressed toward many physiologic races and toward several different diseases, is the goal of the breeder.

Very effective techniques of infection have been introduced into practice in recent years. Artificial inoculation of rusts, for convenience, is usually carried out in the greenhouse on seedlings. Recent investigations, however, have shown a marked difference between seedling reactions in the greenhouse and plant reactions in the field during the period of maximal infection which, in the case of rusts, usually occurs at the time of heading. Growth and environment have great significance, and accordingly, in work on this problem, much attention must be given to plants cultivated under field conditions.

HAYES and GOULDEN, two of the most competent breeders in America, who have worked extensively in the creation of rust-resistant varieties of wheat, emphasize the disparities between the data on infection in the field and in the greenhouse. In general, it is not necessary to have complete agreement between field and greenhouse data. In the opinion of GOULDEN, there may be two possible reasons for these differences: *1*) additional physiologic races occurring in the field; *2*) lack of correlation between the maturative type of immunity, which shows in the field, and the reactions of plants in the seedling stage. We note, however, that in cases of the most extreme immunity, for example in the practically absolute immunity from powdery mildew in Persian wheat, we have not observed differences between field and greenhouse data.

GOULDEN, NEWTON, and BROWN have distinguished three groups of wheat varieties according to their behavior in the field (in the adult stage), and in the greenhouse (seedlings) with respect to *Puccinia graminis tritici*. The first group of varieties which are quite resistant in the field includes Khapli (Indian emmer), Vernal (Russian emmer), Iumillo (durum wheat), Garnet, Marquis, and Quality—these were identical in reaction in the seedling and adult stages. The second group, of the varieties Hope, H-44-24, Pentad, Acme (both durum wheats) and *T. persicum* displayed significant differences in rust reaction in the seedling and mature stages. The third group, consisting of the varieties Reward, Kota, and Marquillo, showed incomplete agreement of reaction in the two stages.

These facts must be kept in mind in comparing the behavior of varieties of wheat in the field, where stripe, leaf, and stem rusts develop on submature plants after heading, and in the greenhouse where artificial inoculation is carried out, as a rule on seedlings, which in general are more easily infected than older plants.[50]

[50] W. STRAIB, in a recent work, "Ueber Gelbrostanfälligkeit und Resistenz in den verschiedenen *Triticum*-Reihen" (Zeitschr. für Pflanzenzüchtung, 18 [2-3] 1933) has published data on the infection of stripe race, *Puccinia glumarum tritici*. His infection experiments were carried out on seedlings in the greenhouse. The author has drawn the general conclusion that among *all species of wheat* there are resistant as well as susceptible varieties with respect to one or another of the 14 physiologic races.

In our field investigations (1911-1918) *a number of species*, such as the single-grained hard wheat (*T. durum subsp. expansum* Vav.) showed immunity in all varieties. With leaf rust and powdery mildew, under field conditions, this was even more marked, and we

By inbreeding with cross-pollinated plants, it is possible to obtain more resistant forms than the parent variety, when dealing with narrowly specialized parasites. Thus in corn, GARBER and QUISENBERRY have obtained, in this way, lines of corn with greater resistance to smut, *Ustilago zeae.* HARLAND, in the same way, obtained varieties of Sea Island cotton that were more resistant to *Bacillus malvacearum* than the parent varieties.

In inbreeding sugar beets, forms have been isolated that are more resistant to *Cercospora* and mosaic than the original varieties, as shown by STEWART in the United States and GRINKO in Ukraine.

In relation to narrowly specialized parasites, immunity usually appears to be a varietal character. Different varieties within the limits of a species are characterized by given degrees of resistance. This is particularly well seen in the reactions of cereals to stripe rust and to different species of smut.

The distribution of immunity shows clearly that often extreme contrasts in immunity or susceptibility may characterize different species of a genus. Therefore, in the creation of the most resistant forms it is particularly valuable to obtain distant crosses. In this connection, among the wheats the most nearly immune to the whole complex of diseases appears to be the single-seeded *T. timopheevi,* which is quite isolated, systematically, from the species of common and durum wheats. Among oats a high degree of immunity from smuts and rusts is found in the Mediterranean species, *Avena byzantina,* and also in the sand oats, *Avena brevis* and *A. strigosa.* Immunity to *Phylloxera* and mildew is found principally in American grape varieties which comprise a distinct group of species. A number of wild species of cotton, including *Gossypium tomentosum,* are resistant to wilt and bacterial blight.

Thus, at the outset, hybridizations between distantly related forms are particularly attractive for the creation of immune varieties. With respect to plants that are vegetatively reproduced (grapes, tree fruits, berries, and potatoes), the use of distant hybridizations, giving the most radical solution of the problem of group immunity, deserves particular attention. Considering the occurrence

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concluded that there was a connection between the phylogeny of the species and their reactions to specialized parasites. This conclusion we later verified on many plants in relation to different diseases, and we have used it, as have many other authors, for the practical purposes of breeding.

The presence of physiologic races complicates the question, but does not disrupt the phylogenetic differentiation of plants, as STRAIB has assumed, since parasites which become more narrowly specialized in their races show a more exact reactivity.

Also in our work with stripe rust of wheat (1911-1918), before the question of races had yet been worked upon, there appeared an even greater degree of specialization under field conditions. Half of the varieties (*i.e.,* thousands of varieties) of common wheats were resistant to this disease in the field, and for the purposes of phylogeny, stripe rust of wheat in our early reactions was too sensitive a reactor, hence for the purposes of phylogenetic differentiation of wheat species, we also used other parasitic fungi, principally leaf rust and powdery mildew, using stripe rust only as an adjunct to these other parasites.

Of principal significance to the breeder is the behavior of varieties under ordinary field conditions during the period when the parasitic fungi develop in the field. Differences in the greenhouse, with artificial infection of different races of fungi on seedlings, must be used with caution for purposes of breeding. The contrast of environmental conditions in field and greenhouse may elicit different behavior in a given variety.

We are recounting these facts and opinions, which at first glance appear to be contradictory, in order to show how complex the reports on parasitism and immunity have become as a result of investigations of the last 15 years.

A study of recent literature on the division of parasites into physiologic races, and a comparison of the reactions of species and varieties of cereals toward races of parasitic fungi, bring out still more clearly the significance of phylogenetic differentiation for the explanation of the several types of reaction (*cf.* the works of REED, CALNICEANU (1933), KIRCHNER, and others).

of a large number of distinct species among the majority of vegetatively propagated plants (*Prunus, Pyrus, Malus, Amygdalus, Vitis, Solanum, Fragaria, Rubus, Ribes*) and, what is even more important, considering the great differences between species in reaction to different parasites, there is particular promise in the use of distant crosses with crops that may be vegetatively propagated.

For species of tobacco, which may be easily crossed, interspecific hybridization opens up interesting perspectives in the field of immunity, the more so since a low production of seeds as a result of crossing does not have great significance in the case of this plant because of the small requirement of seed for plantings.

The matter is more complicated in using distant crosses with plants that are propagated by seed; with plants which are propagated vegetatively we may disregard seed production, but with those plants such as cereals where the yield of seed is of prime importance, first attention may be given to the maximal use of closely related combinations of parents which produce fertile progeny. For example, with wheat great interest attaches to the use of all the varied species and geographic groups belonging to the 28-chromosome group of wheats.[51] For cotton, the species *Gossypium purpurascens* Poir. has particular importance in breeding for immunity. In crossing species of wheat with different numbers of chromosomes in order to obtain forms which combine immunity with other valuable characters, it is necessary to conduct the hybridization work on a very broad scale, with a large number of plants in F_2 and F_3 generations.

Dr. D. Kostov has introduced a new method for obtaining fertile progeny that is useful for plants having even multiples of numbers of chromosomes (polyploid series), namely the inter-hybridization of several (three or four) species to obtain polygenom hybrids. This method has already given interesting results with tobacco. Its use with wheat still requires much work to bring out the most useful components. Concentrated investigations are needed in this field of work. There is particular theoretical interest in the possibility of obtaining immune forms by restoring fertility in hybrids of widely separated parents through doubling the number of chromosomes, the method of Jorgensen, or by other methods, as displayed in a series of hybrids of cabbage × radish, wheat × rye, wheat × *Aegilops,* and species of tobacco (G. D. Karpechenko, E. Chermak, D. Kostov, Egiz, Ternovskii, and others).

The most difficult problem in breeding for immunity is the necessity for combining, in a single variety, both group immunity to many diseases and the other valuable characters such as high yield and quality.

8. **Varietal Resistance of Plants to Insect Attack:**— Differences in varieties and species of plants in resistance to insects has long been used practically in the cases of tree fruits and grapes. In general, insects are less specialized on host plants than are parasitic fungi of viruses; they are less discriminating as to species or even genera of plants. Nevertheless, a considerable number of injurious insects, particularly aphids, scale insects, flies, and plant bugs, are adapted to definite genera and even species of plants, *i.e.,* are monophagic, and may distinguish the varieties within the limits of given species of host plant. Monophagy is also frequent among the different groups of beetles; for example, this applies to a number of species of grain weevils, *Bruchidae,*

[51] For details see the book, N. I. Vavilov, "Scientific Bases of Wheat Breeding," Selkhozgiz, 1935.

and of *Halticinae*. The majority of grain weevils are adapted to single host genera (D. A. SMIRNOV, 1912).

From monophagy, narrow specialization, the entomologist distinguishes *polyphagy,* embracing a wide circle of hosts of very diverse families, and *oligophagy,* adaptation to a more restricted host cycle (WARDLE). Oligophagic insects appear to be plastic in the sense of adaptation to plant species; the selection of host plants in this case relates to the environmental conditions and the presence of this or that wild or cultivated species. In south Germany 35 years ago, the corn borer destroyed hops and hemp; today it has passed to corn, and here it produces little damage on this plant, even in those cases when it develops in corn fields. In other cases insects may have a wide host range in one part of the year and be limited to a few related species in another part of the year, *i.e.,* may show *seasonal oligophagy.* This is true of many species of aphids (*Aphis*).

Recent investigations have shown that in monophages there is a further differentiation into biological races within the limits of a given insect species, the races being externally indistinguishable but adapted to definite species of host plant and even to certain groups of varieties. The investigations of PAINTER in Kansas have shown the presence of two biological races of Hessian fly, one of which is primarily found on the mealy, red-grained, soft winter wheats, while the other principally attacks the vitreous winter wheats which are cultivated to greatest extent in central Kansas. Different races of *Phylloxera* (*vastatrix* and *vitifolii*) has been distinguished. The North American fruit fly, *Rhagoletis pomonella,* may consist of biological races adapted to hawthorn and to apples (WARDLE). N. A. KHOLODKOVSKII has found biological species among aphids of the genus *Chermes.*

In relation to the attack of plants by insects, to even a greater extent than with infection by parasitic fungi, a leading role is played by *external conditions,* both unrelated to man (weather, soil), and those conditions which are created by man's activities (time of sowing, irrigation, etc.). A decisive factor in the attack of insects frequently is a coincidence in the critical phase of development of the plant and the period of greatest activity of the injurious insect.[52]

This sort of phenomenon, in which the plant escapes attack by the parasite and which is unrelated to the hereditary properties of the plant with respect to the parasite, must be distinguished from immunity, which appears under favorable conditions for infection.[53]

Particular attention during recent decades in the field of varietal immunity to insects has concerned the *grape.* The severe attack of grapes in France and in Germany at the beginning of the second half of the 19th century, in connection with the introduction from America of the *Phylloxera,* attracted atten-

[52] The authors of the book, "Insects Damaging Field Crops," V. P. SHCHEGOLEV, A. V. ZNAMENSKII, and G. YA. BEI-BIENKO (1934) have called this sort of relationship of resistance to external conditions "externally conditioned immunity." N. N. TROITSKII has called it "elusiveness."

[53] As for inoculation of poisons into plants to control insects, or so-called internal therapy (*cf.* the above-cited work of MÜLLER, 1926) we may say briefly that it has been clearly shown that branches of woody plants cut off and placed in solutions of barium chloride, aluminum sulphate, pyridine, and copper sulphate, take up these salts and do not become attacked by sucking insects. MÜLLER (1926) injected 5% solutions of pyridine into apple through openings in the trunk and reported that he disinfested the trees from woody apple aphis. In the experiments of JEPSON (1925) who injected potassium cyanide and carbon bisulphide into stems of tea plants to protect against *Calotermes militaris,* a positive effect was not observed. On the whole, this possibility has little use in practice, particularly in field culture, because of the selective absorption by roots; when these salts are introduced into the soil they are not taken up into plant tissues.

tion to the American species that are resistant, such as *Vitis riparia, V. rupestris, V. rubra, V. berlandieri,* and others used as understocks for the European grapes. The basic work on resistance of the American grapes and the first work on their hybridization with the European grapes are associated with the names of MILLARDET, RAVAZ, and VIALA.

An extensive world bibliography on *Phylloxera* and its control, and also a critical review of present knowledge on control of *Phylloxera* is given in the detailed work of F. STELLWAAG, "Die Weinbauinsekten der Kulturländer" (Berlin, 1928).[54]

European grape growing at the present time is based on the use of American varieties which are distinct in having root systems that are resistant to the *Phylloxera,* and also on hybrids with European varieties (*Vitis vinifera*).

An important practical problem in our times is the creation, by crossing European with American lines, of so-called "direct producers" which will combine resistance to *Phylloxera* with resistance to mildew, and at the same time will not be inferior in yield and quality of fruit to the best European varieties. As has been shown by experience of recent decades, it is not easy to obtain such combinations, despite the fact that European grapes give fertile hybrids in crosses with American vines (*cf.* HUSFELD, 1932). The interspecific hybrids obtained are usually much inferior in quality to the best table and wine grape varieties. The quality of wine and table grapes is no doubt determined by many genes. It is necessary to carry out the work on a broad scale; according to the opinion of BAUR, for Germany alone there is required every year a selection from no less than ten million plants in the second generation in order, after several years, with rigid culling and with the aid of artificial inoculation with mildew and *Phylloxera,* finally to obtain the necessary forms. At the present time in both German and Swiss practice (F. KOBEL, BAUR, HUSFELD), the gradual solution of this important practical problem is planned by first isolating high quality varieties that are resistant to mildew and then, with this as a basis, proceeding to the creation of varieties which, at the same time, are resistant to *Phylloxera.* As shown by breeding practice in France, Germany, and Switzerland, the creation of mildew immune varieties is not an easy problem. In the experiments at the Müncheberg Institute, out of 5,000 seedlings in the second generation of this type of interspecific hybrids, BAUR obtained only a single plant which combined immunity from mildew with a comparatively satisfactory quality of grape. Such hybrids, after breeding, are used by grafting them onto *Phylloxera*-resistant American grapes.

Such mildew-resistant varieties are used in further breeding for *Phylloxera*-resistance in order finally to create "direct producers," varieties that combine resistance to *Phylloxera* with immunity from mildew and with good quality as table and wine grapes. The great extent of the work at the present time may be judged by the fact that at the Müncheberg Breeding Institute in Germany alone, where many other types of plants are also studied, each year there are grown from 5 to 7 million seedlings of the second generation. Workers at this institute are now working primarily to develop resistance to mildew. At the present time the Odessa Station is working on a similar scale.

The breeding work in the past has resulted in the development of "direct producers" which at present are widely used in the regions most subject to fungus diseases, such as the northern part of France and the Ukraine, where such grapes are principally cultivated, but until recently the "direct producers"

[54] See also N. N. TROITSKII, "The Phylloxera Problem in Central Europe." Trudy po Prikl. Entom. XV (1), Leningrad, 1929

have not been satisfactory in the quality of their fruit. The French specialists (for example, RAVAZ and others), as we learned by personal conversation in 1927, have been skeptical regarding direct producers, despite the great expense of grafting and of spraying the European grapes to combat mildew and other diseases. In the opinions of BAUR and KOBEL, the failure of breeding in the past has been due principally to the insignificant extent of the work and the use of the unsatisfactory first generation or back-crosses of the first generation with European grapes. Where the second generation has been used, this has been done on entirely too small a scale.

The nature of immunity of the American grapes, despite its more or less extensive study, is far from being clear. Anatomically the roots of the American grapes are quite distinct from those of the European grapes: in the former there is more rapid lignification, the bark is thinner, the structure is more compact, the number of medullary rays is greater, the rays themselves are narrower, and galls do not penetrate deeply within, but are isolated by a cork layer which develops more rapidly than in the European grapes. MILLARDET determined that wounds in American grapes heal more rapidly.

A number of authors, beginning with BOUTIN (1876) and extending up to AVERNA SACCA (1910) and COMES (1916), associated immunity with the high acidity of species of American grapes in comparison with the European grapes. The more resistant the varieties of European grapes, the greater the acid contained in the cell sap.

According to PETRI, the matter is somewhat more complicated. The species *Vitis berlandieri, V. rotundifolia, V. cordifolia,* and *V. coriacea* in this respect are marked exceptions.

ZWEIGELT showed further that the tannins do not have any particular protective value as was assumed by other authors.

The Italian investigator PETRI, who has studied the question of the nature of immunity of grapes most thoroughly, denies any decisive role in immunity of anatomical and chemical petuliarities of the American species. He considers *the cause of immunity tp be the complicated effect of a series of physiological and histological factors specific for species and varieties in relationship with the conditions of the environment.* This view is shared by the majority of the most competent investigators (BÖRNER, STELLWAAG, THIEM, DYCKERHOFF, SCHMITTHENNER, and others).

In any case, from the recent work (RASMUSSON, KOBEL, BAUR, HUSFELD) it is clear that immunity from *Phylloxera* as well as from mildew follows MENDEL'S law in segregation, and may be combined with various varietal morphological, and physiological characters. In RASMUSSON'S experiments (1914), immunity from *Phylloxera* was dominant over susceptibility.

MUMFORD has distinguished two kinds of insect-resistance in plants, *epiphyllaxy* which is based on the presence of external defenses (cuticle, wax, etc.), and *endophyllaxy* which is associated with the biochemical properties of the variety, the presence of organic acids in the cell sap, or the presence of ethereal oils or alkaloids which repel insects. An example of epiphyllaxy is seen in varietal differences in citrus fruits. Thus, in Florida all of the varieties of citrus with thin rinds, such as Mandarin (*Citrus unshiu*) and tangerine (*Citrus nobilis* var. *deliciosa*) are strongly attacked by plant bugs, *Nezara viridula* L. Less attacked is the sweet orange (*Citrus sinensis*), while most resistant of all is the thick-rinded grapefruit (*Citrus grandis*).

Thick-skinned varieties of apples are less attacked by *Rhagoletis pomonella* than are thin-skinned varieties (WALSH). In general, varietal resistance to insects is most frequently associated with structural peculiarities.

The significance of organic acids as protective substances against insects has been emphasized particularly by the Italian investigator Comes in his book "La profilassi nella patologia vegetale" (1916). Mumford found that resistance to the attack of termites, *Coptotermes formosanus* Shir., in some woody species is due to chemical features of the wood.

Many factors associated with resistance are characteristically found in wild relatives of cultivated plants such as a high content of organic acids, bitterness of the fruits, and thick skin of the fruits, and since such characteristics must be eliminated in breeding, this makes it more difficult to create varieties which are resistant, and at the same time have high quality. This hampers breeding for immunity in a number of kinds of plants.

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A number of investigations have been carried out recently on *resistance of varieties of apples to woolly apple aphis* (*Eriosoma lanigerum* Hausm.). Entomologists consider that the woolly apple aphis came to Europe from America where it formerly included in its life cycle development on the American elm (*Ulmus americana*). In America the woolly apple aphis lives through the fall, winter, and spring on the elm as wingless generations. In the summer, winged individuals fly to the intermediate hosts which appear to be endemic species of American wild apples, and also the European cultivated varieties of apples and other genera of the *Pomoideae*. On the intermediate host, during the summer, there develop a number of wingless generations of parthenogenetic females; in the fall, among the latter, there appear winged forms which fly back to the elm.

In Europe the woolly apple aphis develops exclusively on the intermediate host, *viz.*, the apple.

Ordinarily the woolly apple aphis develops on different species of apples which are widely cultivated and used for grafting and also on the less common wild endemic species of America, such as *Malus coronaria, M. ioensis, M. rivularis,* and *M. angustifolia.* It also attacks *M. baccata* and *M. paradisiaca* as well as the European wild apple *M. silvestris* and apples of eastern Asia such as *M. spectabilis* and *M. floribunda.* Only the Chinese apple, *M. prunifolia,* is resistant.

Among the cultivated varieties, a number appear to be distinguished by a significant degree of resistance: among them is Northern Spy which was developed in America, and also a hybrid from Australia. It is noteworthy that the latter variety is characterized by resistance to woolly aphis not only in Australia, but also in England, Argentina, Germany, and France.

For various widely separated regions there are lists of more or less resistant varieties. Extensive investigations on woolly apple aphis have been conducted in New Zealand where there have been discovered a number of resistant varieties. For SSSR the resistant varieties include: iron apple, a number of old Circassian varieties from Caucasus, "kandil-sinap," French rennet, Canadian rennet, pineapple rennet, long-stemmed "kandil," Portuguese rennet, Danzig ribbed, white rosemary, and others. The following varieties are strongly attacked in Russia: white "kalvil," English rennet, winter golden Permain, paper rennet, Napoleon, golden "semyachko," Paradise, and others (L. Porchinskii, Mokrzhetskii, Mordvilko, Nevskii, and others).

The degree of susceptibility of apples to woolly apple aphis is determined by the average extent of swelling of the tumors; in immune varieties tumors are not formed.

The prevailing opinion that the most resistant forms of apples are the acid

varieties is not confirmed in testing large assortments of varieties. The nature of immunity from aphis, in the opinion of a number of authors, is based on the presence of certain specific substances which inhibit the development of the insect (*cf.* Roach, Massee, Monzen); other authors (Staniland) associate immunity from woolly apple aphis with the quantity of sclerenchyma in the cortex of apple branches. In general, the nature of immunity from woolly apple aphis is insufficiently explained. Not infrequently there are observed differences in the damage by the woolly apple aphids to roots and stems of the same variety. There are known to be cases of susceptible root systems with comparatively resistant stems and vice versa. This complicates the selection of resistant varieties. For combatting the woolly apple aphis, susceptible varieties of apples are grafted onto resistant understocks. In view of the fact that strongly resistant varieties such as Northern Spy and Winter Majetin are inferior, as understocks, to Dusen and Paradise, English breeders in particular, considering possibilities for vegetative propagation, have hybridized Northern Spy and Dusen with other varieties and obtained new, interesting hybrids. Immunity from woolly apple aphis, in this case, is evidently dominant (*cf.* the works of the Experiment Station in East Malling, England).

A number of authors (L. P. Simirenko, Grebnitskii, V. V. Pashkevich, Ryaboi, Mokrzhetskii, Sevastyanov, Rikhter, Shchegolev, Parfentev, and others) have demonstrated differences in apple and pear varieties in attack by the *leaf roller.* The greatest attack has been observed on Belle Fleur, white "kalvil," spotted "borovinka," winter golden Permain, pineapple rennet, English rennet, "tsiganka," and others. The most resistant are Mammoth, red Permain, "boiken," London pippin, Simirenko rennet, champagne rennet, "skrizhapel," and others.

N. A. Grossheim, who has most thoroughly studied differences in attack of varieties by the leaf roller, with particular attention to techniques, has brought out numerous causes for the differences in attack, including differences in chemical composition of the fruits, anatomical-morphological peculiarities such as structure of the skin, the pulp, the vascular tissues, the calyx, and the seed cavity, quantity of seeds and parthenocarpy, and hairness of the fruit. He has also shown the significance of the position of the fruit, the degree of coverage of the fruit by leaves, the presence of fruit on the ends of one-year-old branches, and the ability to produce corky tissues. Varietal differences in all cases are according to Grossheim's data, to a whole series of factors.

N. A. Grossheim also determined the differences in degree of attack of apples by snout bettles and by the *Nitidulidae* attacking apples.

Grossheim's work is particularly valuable in showing the necessity for giving great attention to the methods of studying attacks on woody fruits, the necessity for testing resistance on a large number of trees, for use of an extensive assortment of fruits, for considering productiveness of the tree, and for comparing the degree of attack of different varieties in different years. The basic requirements in methods are: *a*) a level terrain; *b*) a uniform productivity in the series of trees; *c*) high yields; *d*) a sufficient quantity of trees to give data of the required extent; and *e*) a sufficient concentration of the insects.

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By interspecific hybridization of pears, *Pyrus communis* and *P. sinensis,* there have been produced forms that are resistant to the San Jose scale (cited by Wardle).

In citrus fruits there is particular resistance to the San Jose scale, *Aspidio-*

tus perniciosus, in *Citrus trifoliata,* which is used in the grafting of mandarins and sweet oranges.

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With regard to resistance of varieties of *field crops* toward insects, comparatively little has been done, particularly in comparison with work on immunity from fungus and virus diseases. This area of breeding and entomological work deserves more attention.

Of the literature available on resistance to insect attack, we have the work of McCOLLOCH (1924) and the well-known book of WARDLE, "Problems of Applied Entomology," where there is a chapter on resistance of the host plants to insect attack (1929). Scattered data on the resistance of different varieties and species are frequently encountered in the agronomic and entomological literature (*cf.* Review of Applied Entomology).

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Among the detailed older investigations on cotton there is the work of the well-known American cotton specialist, O. F. COOK (1906), on the resistance of cotton varieties to the boll weevil. In Guatemala, where the boll weevil is very abundant, COOK found an Indian woody cotton, Kēkchi, which was resistant to this insect, or at least only very weakly attacked. This dwarf, rapidly growing, annual cotton resembled externally the rapidly-growing, well-known upland variety King. Kekchi was distinguished by a satisfactory quality of the fiber and comparatively high yields. The work of HARLAND in Trinidad is also particularly valuable. He produced forms resistant to the cotton mite, *Eriophyes gossypii* Banks, which causes the formation of galls in which the mites live. Upland (*Gossypium hirsutum*) and Egyptian cotton (*G. barbadense*) as well as the ordinary Sea Island, were attacked very strongly. The resistant varieties were principally derived from West Indian and Brazilian local forms belonging to the species *G. purpurascens,* Bourbon cotton, with characteristic smooth bolls, and perennial, monopodial habit. In crossing the resistant and susceptible forms there was observed a clear-cut segregation. The F_1 was intermediate; the immune forms appearing in the F_2 remained constant in further generations. The most susceptible forms remained constant in later generations while the intermediate ones segregated and often gave entirely immune ones.

Cotton varieties with hairy leaves, for example a number of upland cottons, according to the report of WORRALL (1924) in South Africa, are more resistant to attack by leaf hoppers (*Empoasca facialis* Jacob.), than varieties with smooth leaves (Egyptian and Sea Island).

The cotton variety "U-4," developed by PARNELL, is highly resistant to leaf hoppers and is grown as a standard variety in South Africa (Rhodesia). HARLAND found in Trinidad that all of the smooth-leaved varieties of New World cottons were strongly attacked by leaf hoppers, while, at the same time, the Old World Asiatic cottons were either entirely unaffected, or attacked only weakly. The variety called "U-4" behaved just as in Africa. The Peruvian perennial cotton, Tanguis, with hairy leaves, which is systematically close to the Egyptian and Sea Island cottons, was also resistant to leaf hoppers. Hybrids of Tanguis crossed with smooth-leaved upland cotton, having an intermediate degree of hairiness, were frequently resistant (HARLAND).[55]

On the other hand, in relation to the cotton thrips, the hairy upland cottons

[55] In the investigations of AINSWORTH (1931) on the closely related species, *Empoasca fabae* Harr., which develops on the leaves of legumes, no relationship was observed between attack and hairiness.

were more susceptible than the smooth leaved Egyptian cottons (WARDLE and SIMPSON, 1927). BURT and NIZAMUDDIN HAIDER found that susceptibility to *Aphis* was associated in cotton with smoothness of the leaves.

Sea Island and upland cottons from the West Indian islands are often attacked by the scale insect, *Saissetia nigra.* HARLAND found that bourbon cotton (*G. purpurascens*)—Serido from Brazil—was entirely immune from this scale: hybrids of it with Sea Island also showed complete immunity. This was shown in a particularly striking fashion by grafting susceptible Sea Island onto immune understocks. All parts of the immune variety (branches and leaves) remained unattacked; while all parts of the susceptible variety were strongly attacked. The reverse experiment of grafting an immune variety onto a susceptible one showed comparable results.

A good many investigations have been carried out with *cereals.* PARKER, SALMON, and other investigators in Kansas have found a marked difference in the reactions of sorghums to the chinch bug. All sorghum varieties of the Milo group were attacked by the chinch bug under Kansas conditions, while varieties of Kafir, for example Atlas, Orange Kansas, and Blackhull, showed a considerable resistance. Hybrids of the first generation between Milo varieties and Kafirs were resistant; in segregation in the second generation there appeared even more resistant forms than the original parents. PARKER considers that the resistance in this case is evidently due to anatomical features.

MARSTON in Michigan (U.S.A.) found that the corn variety Armargo (obtained from South America), according to his observations, was resistant to the corn borer. Crossing it with local Michigan corn varieties he obtained a number of new resistant varieties. Resistance in this case acted as recessive.

The polyphagy of the corn borer, which attacks hundreds of species (including beans, hops, hemp, and millet), compels us to be rather careful in interpreting the "resistance" of corn varieties. It is possible that the damage by the corn borer to the variety Amargo may be less because of features of its growth, leafiness, etc. Observations on a great many varieties of corn in Russia have not revealed noteworthy varietal differences in reaction to the corn borer.

COLLINS and KEMPTON (1907) found varietal differences in corn with respect to the corn earworm, and developed resistant sweet corns. GERNERT (1917) showed that hybrids between corn and teosinte are resistant to the corn aphis.

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Varieties of *wheat* differ in attack by larvae of the beetle *Lema melanopa* L. in relation to the character of the leaves. Hairy wheats are attacked less than smooth-leaved forms (V. A. MEGALOV).

According to the data of V. SHCHEGOLEV, wheats having solid straw (for example some of the durum wheats) are less attacked by the grain saw fly (*Cephus pygmaeus* L.) and the black saw fly (*Trachelus tabidus* F.) than ordinary wheats which have entirely or partly hollow straw. Among the solid-strawed wheats in the world collection, varieties from Algeria were particularly noteworthy when, during four years' testing they were entirely free from attack. Early-maturing varieties of cereals, although they are attacked by saw-flies, usually suffer less reduction in yield.

Many investigators have noted the resistance of certain varieties of wheat to Hessian fly (PACKARD, 1883, WOODWORTH, 1886-1889, ROBERTS, SLINGERLAND, STONE, 1901, GOSSAD and HOUSEN, 1906, ZNAMENSKII, A. V., 1926, and others).

Comparatively extensive investigations on the resistance of wheat to Hes-

sian fly (*Phytophaga destructor*) have been conducted in recent years by McColloch, Parker, and Salmon in Kansas. Testing about 400 wheat varieties they found a number of resistant winter forms, such as Michigan Wonder, Red Rock, Fulhard, Honor, Illini Chief Sel., Dawson, Golden Chaff, Kawvale, and Purkof. On the other hand the wheats commonly grown in Kansas were strongly attacked, such as the varieties Kanred, Minturki, Kharkof, Turkey Nebraska No. 6, Burbank, Tenmarq, and Iobred. Some of these latter have come from our region and are typical Ukrainian and Crimean winter wheat varieties. The varieties Blackhull and Red Winter occupied an intermediate position. Unfortunately the majority of the resistant varieties were rather unsatisfactory in other qualities. Common wheats were attacked by the Hessian fly to a somewhat greater extent than durum wheats (V. G. Batirenko, A. Kirichenko, D. Znioko, and others). According to the investigations of A. V. Znamenskii in Poltava (1926), the durum wheats, on the average, were affected to the extent of 14.9% and the common wheats 75.5% of the plants. The infestation on stems for durum wheats, was 11.1 and for common wheats 60.3%. This is explained by the fact that the Hessian fly attacks both kinds of wheat in egg-laying, but in later development a number of the larvae on hard common wheats evidently die. The cause of this phenomenon has still been insufficiently studied. *Triticum monococcum* in Odessa is entirely resistant to Hessian fly (D. Znoiko).

Hybridization experiments have shown that resistance to the Hessian fly is inherited, is conditioned by many factors, and may be combined with such characters as quality of the flour, winter hardiness, earliness, and non-lodging (Parker, D. Znoiko, and Kirichenko). Varietal differences in reaction to Hessian fly evidently are not associated with morphological differences as was assumed earlier, but with peculiarities of the chemical composition of the plasma or cell sap (Parker, Kirichenko, and Znoiko), and with a selective power on the part of the Hessian fly.

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According to data from the Russian system of variety testing, the durum wheats are attacked by the frit fly *Oscinella frit* L. more than varieties of common wheat. There has been observed an extensive gradation of types of resistance to this insect.

Varieties of barley are sharply distinguished by their resistance to attack by the frit fly. The most resistant (*i.e.,* the least attacked) appear to be forms of the type of two-rowed, Trans-Caucasian barley, *colchicum,* according to R. E. Regel. These have a peculiar bushiness with a large number of equal tillers, and are almost totally resistant to the frit fly. On the other hand, the broad-headed few-stemmed, naked-grained barley, (*vulgare coeleste*), which is cultivated extensively in the mountainous regions of Central Asia, is very strongly attacked by the frit fly. These varieties are even more strikingly differentiated by the attack of this insect on the heads (N. N. Troitskii). The group of two-rowed barleys is hardly affected under field conditions (Leningrad), while at the same time the group *vulgare coeleste* is attacked with extreme severity. The work of entomologists at the Detski Village Station (N. N. Troitskii) has shown that, in comparison with other barleys, the two-rowed Caucasus forms (*colchicum*) are attacked to a very small extent by the frit fly during the seedling period, and practically not at all in the heading period. In addition, the Caucasus two-rowed barleys are able to branch energetically from the first and second basal nodes. This characteristic provides more resistance to damage by the frit fly.

According to data from Saratov (N. L. SAKHAROV) the *colchicum* barleys are also relatively resistant to the frit fly under the conditions of the southeastern European part of SSSR. Varietal differences were also noted for wheats, but these were all attacked to some extent, particularly when they were transferred from other regions. Thus the hard wheat, *melanopus* 069, which was entirely resistant at the Ural Station, was attacked at Saratov to the extent of 16.4%. This fact possibly may be explained by the generally weaker development of the frit fly near the Ural Station.

CUNLIFFE (1925) has noted that some varieties of oats in England are comparatively resistant to damage by the frit fly because of their rapid growth and energy of tillering.

Among our ordinary oats varieties, according to the data from the Russian variety testing system, resistant forms have not been found.

The question of varietal differences among wheats in attack by the frit fly has not yet been satisfactorily worked out. According to the data from the Russian variety testing system, all of the ordinary local common wheats used in breeding were without varietal differences in this respect.

Usually in SSSR barley is most severely attacked by the frit fly, followed by durum wheats, common wheats, and finally oats. In western Europe, the crop most severely attacked is oats, while barley is damaged least. In North America the most severely attacked crop is wheat. In the Far East the frit fly behaves with us as in America, but in White Russia and North Caucasus, as in Western Europe (A. LYUBISHCHEV, 1933). The decisive factors, in the opinion of A. LYUBISHCHEV, are factors contributing to vigorous growth, particularly moisture. Under the moister conditions, oats are most strongly attacked, and under drier conditions, barley.

The new species of wheat, *Triticum timopheevi* Zhuk., which is distinguished by the high degree of hairiness of its leaves and leaf sheaths, is outstanding in its resistance to the frit fly under conditions of heavy attack on wheat in the Maikopsk Region of North Caucasus. Both stems and grain, according to observations of YA. S. AKSININ, are resistant to attack. Under the conditions of Detski Village, near Leningrad, *T. timopheevi*, in date-of-planting experiments invariably showed its comparative resistance to the frit fly, particularly from first and most susceptible period of growth up to the beginning of tillering. Later attack, although it does occur, does not have much significance (CHESNOKOV, P. G., 1934). This species deserves particular attention from the breeder, especially since it is also resistant to a number of fungus diseases. The resistance of this species to the frit fly is particularly interesting, since it is a later spring variety such as are commonly severely attacked by the flies.

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N. L. SAKHAROV has found that wheat varieties are quite distinct in their resistance to the spring fly, *Phorbia* (*Adia*) *genitalis* Schnabl. Durum wheats are resistant, common ones susceptible. The resistance is determined by the structure of the leaf sheath: the more tightly it surrounds the straw, the less will the wheat be attacked by the fly. The tightness of clasping is determined, in turn, by the structure of the ligula. Eligulate forms are most severely attacked. The significance of the tight clasping of the sheaths is explained by the fact that in forms with a well-developed ligula the fly is unable to insert its ovipositor into the sheath in order to lay eggs. Hairiness of the leaves favors attack. The more rapidly and more energetically the stems develop, the less damage will the plants sustain from fly injury.

An excellent investigation of the resistance of barley varieties to the cereal nematode, *Heterodera schachtii,* has been carried out by NILSSON-EHLE in Sweden. He found a number of varieties of two-rowed barley which were distinguished by resistance to the nematode. These included Khankhen, Chevalier I, Chevalier II, "Lebedinaya Sheya," and Primus. Local Swedish varieties, particularly 4-rowed varieties, were quite susceptible. Hybridization experiments showed that inheritance of resistance followed MENDEL's Law. In a number of combinations, in the F_3 and F_4 generations, there was observed a simple ratio, approximately 3:1, with immunity dominant over susceptibility. Resistance could be combined with other characters. The crop most severely attacked by nematodes in Sweden is oats, which is customarily grown in rotations after barley. The introduction of resistant varieties of barley reduced infestation of nematodes in the field and increased the yields in subsequent oats culture.

Varieties of *red clover* are distinguished by resistance to attack by *Empoasca fabae* (*cf.* JEWETT, H. H.).

From among the varieties of *cowpeas* (*Vigna sinensis*) ORTON selected the variety Iron for freedom from attack by nematodes, *Heterodera radicicola;* resistance in this case, as in that of NILSSON-EHLE, was dominant over susceptibility.

A particularly well-understood case of immunity is that of the *sunflower* from the sunflower moth (*Homeosoma nebulella*), which is due to the presence in the seed coat of a protective layer consisting of dark-colored cells with peculiar chemical composition, principally consisting of carbohydrates (up to 76%). In the ordinary susceptible sunflowers, in a cross section of the seed coat one observes epidermis, corky layer and sclerenchyma. In the protected sunflower there are epidermis, corky layer, protective layer, and sclerenchyma. The formation of the protective layer of the seeds occurs after fertilization. On the third or fourth day after fertilization one may observe the formation of a membrane which develops into this layer under the corky tissue of the seeds. N. L. SAKHAROV (1925) has shown that the moth, in its egg-laying, does not distinguish between the protected and the ordinary varieties. Thereafter, however, in the protected varieties, the protective layer of the seedcoat develops before the larvae begin feeding on the seeds. The larvae are unable to gnaw through the protective layer of the seed and only scrape off the epidermis and corky tissues. The protective layer, particularly when it is well developed, thus saves the seed from being eaten by the larvae of the sunflower moth (*cf.* E. M. PLACHEK, N. L. SAKHAROV, SATSIPEROV, and others). HANAUSEK, who has carefully studied the nature of the protective layer and its chemical composition, has called it "carbogenic," so-called because of the great quantity of carbon. This layer protects the seed both from parasites and from drying out. Of 278 *Compositae,* 98, according to the investigations of HANAUSEK, showed a carbonaceous protective layer. In the tribe *Heliantheae* all of the genera, without exception, were provided with this layer.

It is noteworthy that often the protected varieties are at the same time resistant to broomrape. This correlation is not absolute, but in all cases among the groups of protected sunflowers there appear many forms that are immune from broomrape. The experiments of E. M. PLACHEK have shown that the protection or resistance to the sunflower moth is inherited according to MENDEL's Law.

Workers at the breeding stations (E. M. PLACHEK at the Saratov Station, ZHDANOV in Rostov, KARZIN in the West Siberian Station, and others) have developed valuable protected oil types of sunflower, and the sunflower moth,

which at one time devastated this crop, has now disappeared from the fields with the introduction of the moth-resistant varieties.

According to the observations of a number of authors (for example, N. L. SAKHAROV, and O. A. PILYUGINA in Saratov) varieties of *peas, vetch,* and *lentils* are sharply differentiated in the attack of the legume snout moth (*Etiella zinckenella* Tr.). The attack on the grain, under uniform field conditions varies in the different varieties from 0.1 to 59.3%. The resistant varieties of peas include the varieties Sibirskii and *Pisum sativum vulgare* of the Moscow Breeding Station and also the waxy pea *P. s. vittelinum;* of the lentils, *Lens esculenta* var. *himalayensis* (0.1) and the Bukhara lentil (0.3); of the vetches, *Vicia sativa* var. *typica leucosperma* Sér. and *V.s.* var. *typica melanosperma.*

Extensive investigations have been carried out on varietal reactions of *peas* toward weevils, *Bruchus pisorum* L. Least susceptible under Ukraine conditions were the late blossoming varieties. Varieties with medium and early blossoming gave the highest percent of grain attacked (P. I. KRASNYUK, 1929). Absolute resistance to the weevil has not yet been found in peas. The highest degree of resistance, according to the experiments in Ukraine (I. I. KORAB, 1927), has been found in the Afghan small-seeded pea, *Pisum asiaticum* Govorov. In its egg-laying the pea weevil clearly prefers large-seeded forms of the ordinary *Pisum sativum.* The chick pea, *Cicer arietinum,* is not affected by the legume weevil, which is explained by the presence in the seed coat of oxalic acid salts. The chick pea is also resistant to snout moths, *Etiella zinckenella.*

With respect to attack by insects in the *cabbage tribe,* there is little susceptibility in red-headed varieties. The greatest attack occurs on cauliflowers; an intermediate position is occupied by the white-headed varieties. This applies to flea beetles of the genus *Phyllotreta* (*cf.* V. A. LEBEDEV, 1924), to the cabbage aphis and the cabbage fly, and to the cabbage cutworm (according to the report of N. N. BOGDANOVA-KATKOVA).

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The resistance of plant varieties to insects has been insufficiently studied. The question is complicated by the great effect of environmental conditions, in determining the appearance of variety differences with respect to insect attack, including the micro-climate created by the plants themselves (their leafiness, tempo, and rhythm of growth). The conditions of the environment markedly change the behavior of the insects. For example, the water balance in irrigated culture has great significance, for the development of both the plants and their pests. From experiments in Egypt, it is known that with heavy irrigation the Egyptian clover is severely attacked by aphids. By means of fertilization it is possible, to some extent, to change the reactions of the plants; thus ANDREWS has shown that by means of heavy fertilization of tea plants with potassium and phosphorus fertilizers, their resistance to mosquito blight can be increased. MUMFORD has shown that sodium carbonate and ammonium sulphate fertilization increased the resistance of cabbage to the fly *Phorbia brassicae* (Bouché).

Differences in soil conditions and also in climate play a very essential role in determining the interrelationships between varieties and insects. The problem at present appears to include both a more thorough study of different cases of varietal resistance, and a critical synthesis of the disconnected experiments.

The end goal of breeding along this line appears to be *group immunity,* simultaneously to several diseases, and most of all, at the same time combining immunity to a number of important fungus, bacterial, and virus diseases, with resistance to insects.

A significant number of factors in the distribution of immunity testify to the occurrence of regularities also in relation to insects, just as in relation to parasitic fungi and to diseases. The presence of resistant varieties, or the absence of such, within the limits of a given cultivated plant, in relation to monophagous insects, is determined largely by the degree of biological specialization of the parasite and the differentiation of the host plant itself. The more sharply a given plant is divided into distinct species and geographic groups, or the greater the varietal contrast in morphological and phsiological characters, the greater chance we have of finding varietal differences in reactions to attack by different species of specialized insects.

The data at hand indicated the real possibility of creating group immunity to numbers of diseases and insect pests.

Thus, American species of grapes which are resistant to *Phylloxera* are at the same time immune from mildew. The protected varieties of sunflowers which are resistant to sunflower moth not infrequently are at the same time resistant to broomrape. L. ZHDANOV has combined in one variety broomrape and sunflower moth resistance and high oil content.

The species of wheat, *Triticum timopheevi* Zhuk., is resistant to attack by the frit fly and also has immunity from leaf and stripe rusts, from *Fusarium,* and evidently from loose smut and a number of other fungus diseases.

The Mexican species of wild potato, *Solanum demissum,* as shown not long ago by TROUVELOT, LACOTTE, and THÉNARD, is very resistant to *Phytophthora* and also to low temperatures, and is only weakly attacked in America by the Colorado potato beetle *Leptinotarsa decemlineata.*

In the search for resistant species and varieties of cultivated plants, in some cases an important role may be played by the *introduction* of new species and genera of plants, particularly in relation to narrowly specialized parasitic insects. This must be done under conditions of strict regulation of the introduction of seeds and plants. BODENHEIMER (1926) has shown in the case of cultivated plants from Palestine and other regions, that new crops are characterized by their small numbers of species of damaging insects in those cases in which the crops have been introduced without their parasites. The same thing has been shown by FABRE in the "Instincts and Preferences of Insects," Vol. II, in the chapter on grain insects.[56] The process of adaptation of the local entomofauna to new host plants (excluding the polyphages) in the majority of cases is evidently very slow. Australian and Chinese cultivated plants (*Eucalyptus, Casuarina, Citrus*) are little attacked in new localities even when the plants have become widely distributed. The *Eucalyptus* in Palestine at present is a very common tree, and on it as BODENHEIMER writes, the most competent entomologists "have observed almost total absence of pests. The same applies to *Casuarina.*" The matter is quite different when there are introduced species which are closely related to native plants from which even the most specialized parasites can easily pass over. Species of beans which originally came from Mexico and Central America have very few injurious insects in Europe. The same has been determined for potatoes, which originally came from South America. Although the potato in America is attacked by many species of insects, in Europe it has relatively few insect enemies, according to the report of N. N. BOGDANOVA-KATKOVA.

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The problem for the next few years is a systematic study of the relationships of important cultivated plants, including their species and varietal dif-

[56] See Russian translation, 1914. Petrograd.

ferences, toward different fungus, bacterial, and virus diseases, and pests of the insect world. For given collections of standard breeding varieties there must successively be determined the reactions to diseases and there must be created phytopathological and entomological classifications of varieties and species of important cultivated plants, on the basis of which may be developed the systematic breeding work of the future.

9. **Scales of Varietal Resistance to Infectious Diseases:**— In our book, "Immunity of Plants" (1919), we have considered in detail scales for noting the degree of susceptibility of plants to parasitic fungi. Usually varietal resistance is not absolute, but shows as a greater or less resistance against plant infections. In studying the resistance of varieties to different diseases, we resort to the use of scales of resistance or scales of attack (under optimal conditions for infection).

Along with the ordinary expressions of the degree of attack in percentage of attacked plants, or in percentage of leaf area occupied by the fungus, or by a classification of increments of attack expressing quantitative relationships, we have considered and continue to consider it necessary to supplement the quantitative expression with qualitative features of specific reactions between parasites and plants in different varieties. These specific differences are expressed in the character of killing of tissues, in the nature of the infection, and in its localization. For example, some forms and species of oats are characterized by a definite localization of loose smut infection, exclusively in the stamens; the exterior of the panicles of such oats appears to be entirely healthy. Varieties that are immune from rust usually show definite traces of the antagonism between host cells and the penetration of the fungus into the tissues, which appear as dead tissues or yellow spots.

In relation to external or internal fungus parasites of leaves and stems, we may note the following broad types of relationships between plants and parasites.

1. When plants are entirely immune and no trace of infection is seen even when they are attacked under optimal conditions; spores either fail to germinate on the epidermis, or they germinate and penetrate into the host tissues, but are unable to develop mycelium and normal haustoria in the cells and intercellular spaces. This, for example, is the behavior of *monococcum* wheat or *Triticum timopheevi* when attacked by leaf and stripe rusts.

2. The reverse phenomenon takes place in highly susceptible varieties when the fungus freely invades and infects the plant; the haustoria penetrate deeply into the host cells, and the mycelium forms numerous normal spore pustules; the plant cells that are adjacent to the developing pustule continue to appear healthy, containing chlorophyll and creating the impression that the fungus is not destroying the leaf, but slowly utilizing its host, and even stimulating its cells to a somewhat intensive life activity. In other words, in suitable combinations of fungus and host plant, at the beginning there exists something like a symbiotic relationship.

3. In a few cases of sharply expressed immunity, the fungus penetrates into the host tissues and pale or yellow spots on the leaves or stems indicate the presence of mycelium in the intercellular spaces, and in the cells (in attack by rusts and mildew fungi), so that often very resistant forms of plants, as in cereals and roses, are covered with numerous small yellow and brown spots each one of which represents an infection locus. Either no spores are formed, or if they are formed, they are unable to break through the epidermis to the outside and form pustules, as in the Western European emmers (*T. dicoccum*); sometimes tiny fungus pustules may form on such immune plants.

4. In other cases, which are more frequent, spores are formed and pustules break through the epidermis and are released outside, sometimes in very great quantities, but brown and yellow spots surround such pustules, which are usually somewhat smaller than normal ones, testifying to a killing of the plant tissues at the place of penetration of the fungus, and to a disruption of the normal feeding of cells of the host plant, along with those of the parasite.

There are included two colored plates showing our degrees of resistance to stripe and leaf rusts of wheat (*Puccinia glumarum* and *P. triticina* Eriks.)

Our system for noting the attack by rust species on leaves of mature plants at the ripening period, under optimal conditions for attack, is as follows:

4. *Plants strongly attacked by rust.* The surfaces of the leaves are continuously covered with large pustules. There are no yellow spots of dying leaf tissue surrounding the pustules. (See FIGS 5 and 6).

3. *Plant moderately attacked by rust.* The leaf surfaces are partly free from rust. The fungus pustules on average leaves are very small. In general, they are more scattered, clearly smaller than those of the preceding types, and are surrounded with yellowish or brownish leaf tissues.

2. *Plants weakly attacked.* Separate small fungus pustules scattered over the leaves. A very marked expression of yellow-brown leaf tissues indicates the places of infection by the fungus. Often the pustules are unable to break through the epidermis.

1. *Plants very weakly attacked.* Isolated small fungus pustules on the leaves; very often the pustules are unable to break through the epidermis. Yellow-brown leaf tissues surrounding points of infection.

0. *Complete absence of development of fungus pustules.*

For other fungi the scale must be changed somewhat.

When using such a scale, in our experiments, we consider that this sort of qualitative-quantitative scale is most useful in discriminating varietal differences in immunity. It is natural that in connection with different parasites it must be somewhat varied, but the basic principle of appraisal, combining the quantity and quality of the reactions, is common to all. Such a scale is particularly suitable for orientation with a large varied assortment of varieties.

Some investigators use the scale of MELCHERS and PARKER which considers only the quantity of pustules.

Finally, for a few varieties it is possible and useful to undertake more detailed investigations considering the rank of the leaves and different times of sampling, and with detailed quantitative appraisal. Varieties differ according to the time of appearance of rusts and other fungi, which is a specific varietal character. The American scale of MELCHERS and PARKER considers the degree of coverage of the leaf surface with rust pustules. A maximum value of 100% corresponds to a 37% coverage of the leaf surface with pustules; below this are the values 65, 40, 25, and 10%. This scale has been justly criticized by N. A. NAUMOV (1924). The scale of MELCHERS and PARKER has been modified by L. F. RUSAKOV (1927).

From all that has been said above on the nature of immunity, it is clear that the quantity of the parasite or the quantity of pustules is not the decisive factor. Varieties having a smaller number of pustules may actually suffer more from fungus attack than varieties that are covered with a greater number of pustules.

In appraising disease, one must consider the growth stage and the conditions under which the epidemic develops. It may be that under conditions of artificial inoculation in the greenhouse the statistical method is applicable, but under field conditions we consider that the foregoing qualitative-quantitative scale is most suitable.

For smut fungi, for practical purposes, it is natural to consider the percentage of attacked plants as most suitable, but even here, in respect to smuts of corn, sorghum, wheat, barley, and oats, there appear qualitative differences, expressed in a localization of the parasite and in the behavior of the plant tissues.

Fractional methods of appraisal used by some investigators are very labori-

ous, and hence if they are used this must be limited to a detailed study of a few varieties.

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SCIENTIFIC BASES

of

WHEAT BREEDING

Introduction:— The culture of wheat throughout the world at present occupies an area each year of about 160 million hectares, with 36 million in the Soviet Union. Of the 800-850 million hectares annually cultivated throughout the world, about one-fifth are thus devoted to the culture of wheat. About one-tenth of the wheat acreage is occupied by hard wheat (*Triticum durum* and closely related species), the remainder consists of soft wheat. The area occupied by wheat is first among all crops, and even this has a tendency to increase. From 1910 to 1932 the world acreage increased 23% (more than 30 million hectares) while grain production increased 22%.[57] There has been a significant increase in the acreage in SSSR in recent years. World wheat production reaches a colossal figure, about 140 million tons annually. According to estimates of the acreage suitable for wheat culture in Canada, U.S.A., and SSSR, with the cultivation of new areas wheat culture may be considerably increased—almost doubled. The only area where future expansion appears to be limited is Argentina, where almost all of the pampas suitable for wheat are already cultivated.

The well-known economist-statistician, O. E. BAKER, director of the section of agricultural geography in the Department of Agriculture in Washington, in his interesting publication, "Potential Supply of Wheat" (1925),[58] has determined the world area suitable for wheat culture at 1400 million hectares (5.5 million square miles). In other words, if it were necessary and expedient the acreage cultivated in wheat could be increased several times. A good example of the world possibility of increasing agriculture is that of Canada where the acreage of wheat during the 20th century has been increased twelve-fold. From 830,000 hectares in 1900 the wheat acreage in Canada grew to 10,500,000 hectares in 1933.

Spring wheat is grown extremely far to the north, and ripens normally under our conditions, using the varieties distinguished by early maturity, on the Solovetski Islands (65.5° N. Lat.) and in Palmyra at altitudes of 3500 meters above sea level. In Alaska it is cultivated at the latitude 66° 20′ near Fort Yukon. The limit of cultivating winter wheat without use of vernalization according to the Italian ecologist, AZZI, is the January isotherm of —12° C. In regions with abundant precipitation (particularly snow) the limit of culture for winter wheat is somewhat higher than in continental dry regions.

In the study of the theory of plant breeding, it is particularly important to note that wheat has been the object of greatest methodological study, consisting as it does of a great assortment of varieties and, what is particularly important, of species. One can hardly think of a more suitable object for investigating questions of interspecific and intergeneric hybridization. The occurrence of wild, related species and genera with which wheat may be crossed permits us to go into the question of evolution and undertake the radical modification of cultivated wheats.

No other plant has been used so extensively in breeding as wheat. Using wheat as an example, we can clearly see the features of modern theoretical breeding and genetics and may trace the course of present-day breeding work.

[57] BENNETT, M. K., World wheat crops, 1885-1932. Wheat studies, Vol. 9, 1932-1933, pp. 239-274.

[58] BAKER, O. E., 1925. The potential supply of wheat. Economic geography. Vol. 1, pp. 15-52.

Many of the fundamental principles of the theory of breeding and genetics have been, and continue to be, worked out on wheat.

In beginning a study of the theory of wheat breeding, it is necessary first of all to consider that already in prehistoric times, in different parts of the old world, man was cultivating different species and groups of wheat varieties. Many of the present day cultivated species of hard wheat, for example, the "English wheats" (*Triticum turgidum*), and a great group of Asiatic soft wheats not to mention the einkorns and emmers, have been cultivated for thousands of years. The agricultural civilizations of southwestern Asia, the Mediterranean region, and Abyssinia have selected their own species and varieties of wheat during thousands of years. Even for western Europe, for example England, it has been shown that wheat was cultivated two thousand years before our era.[59] Thus, for thousands of years wheat has been worked upon by generations of recognized and unknown workers. Recent archeological data and botanical-geographical investigations, using the method of differential systematics, have brought out very clearly the antiquity of the breeding process which had subdivided wheat into a large number of species and ecological-geographical groups thousands of years ago.

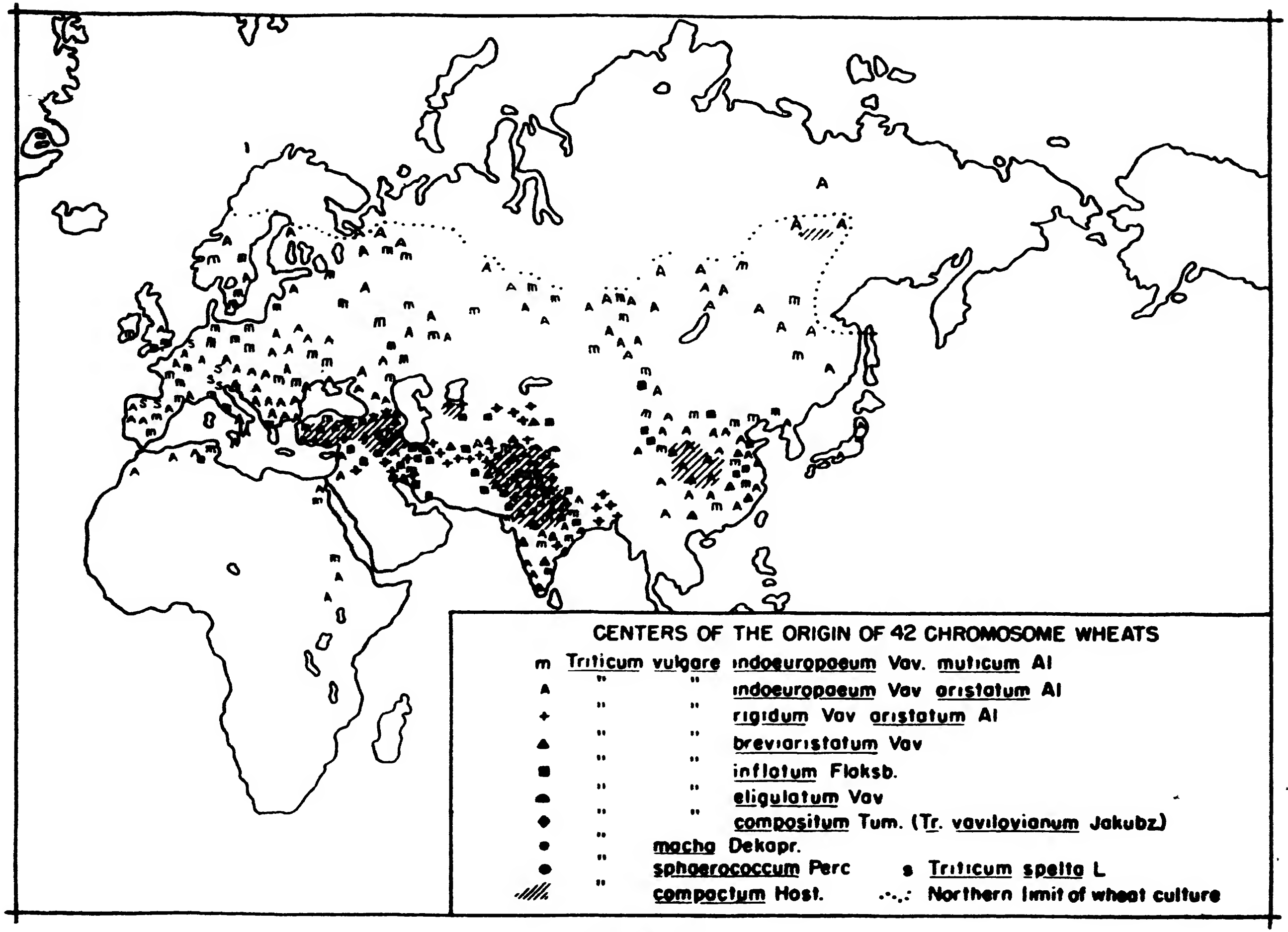
The specific, or more exactly the generic, potentialities of cultivated wheats, scattered over a great area of the Old World, have evolved in prehistoric times. All of the many species of wheat which we have at the present time, have come to us with comparatively little change, out of the distant past, as may be judged by morphological characters. The heads of emmer (*Triticum dicoccum*) found in great quantity in the sarcophagi of ancient Egypt, in external form differ little from present-day Mediterranean forms. Only one of the group of most productive western European wheats, the so-called "squareheads," has been the result of recent times, at least as regards its extensive culture. Its origin is commonly considered to be hybridization between the club and soft wheats. The first mention of the "squareheads" in the European literature goes back only to the beginning of the 19th Century in connection with agriculture in eastern England; its more extensive culture occurred principally in the second half of the 19th Century when it began to be used in breeding in Sweden, Holland, Denmark, Belgium, and Germany. In central China there has also been found an independent group of "squareheads," which probably existed there in earlier times.

There is no doubt whatever that different geographically isolated ancient civilizations of the Old World not infrequently introduced into culture different species and subspecies of wheat. In any case, it is very essential, in approaching the problem of wheat breeding, to have in mind clearly the differentiation of wheat into species and ecological-geographical groups, which is clearly associated, to considerable extent, with the destinies of primitive peoples of the Old World, and with their first emigrations out of the isolated territories which they occupied. This may be perceived most clearly in the examples of Abyssinia, Syria, Egypt, Northwest India, and Trans-Caucasus, which up to this time had been characterized by groups of endemic species of wheat which had not escaped from their original confines.

In the past, as well as in the present, wheat basically is associated with the temperate zone or with the mountainous regions of subtropical and tropical areas that are characterized by temperate climates.

Generic, Specific, and Varietal Potentials of Wheat (The Problem of the Initial Materials in Wheat Breeding):—Theoretical investigations of the

[59] J. Percival. Wheat in Great Britain. Reading, 1934.


CENTERS OF THE ORIGIN OF 42 CHROMOSOME WHEATS
m Triticum vulgare indoeuropaeum Vav. muticum Al
A " " indoeuropaeum Vav aristatum Al
+ " " rigidum Vav aristatum Al
▲ " " breviaristatum Vav
■ " " inflatum Floksb.
" " eligulatum Vav
◆ " " compositum Tum. (Tr. vaviloviarum Jakubz)
● " macha Dekapr.
● " sphaerococcum Perc
s Triticum spelta L
//// " compactum Host.
Northern limit of wheat culture

— Figure 9 —

variation in plants on the basis of the law of homologous series and its general applicability led us to the conviction that our knowledge was very inadequate with respect to the specific and varietal potentials of important cultivated plants, including first of all the wheats with which we began our work.

In 1916 the author began his comparatively extensive expeditions, extending into northern Iran, present-day Uzbekistan, Tadzhikistan, and Turkmenistan, and collected extensive wheat materials which were then investigated in detail in plantings in Saratov and Moskva.

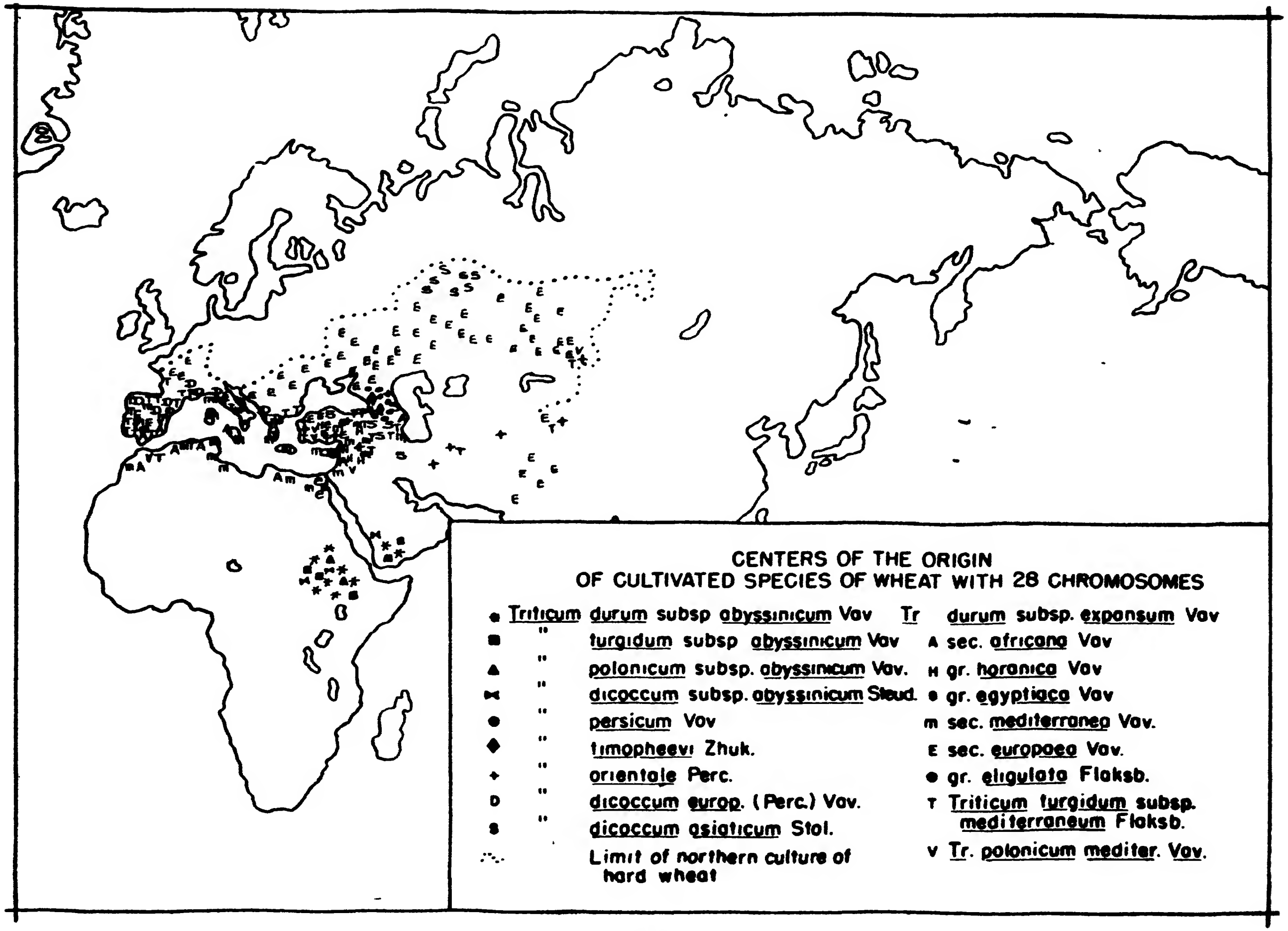
The Institute of Plant Industry in 1923 began an organized series of expeditions in search of diverse forms of wheat which were lacking at that time. On the basis of the law of homologous series it was clear that in nature there must exist a great diversity of wheat forms. At the outset the expeditions were directed to the regions of ancient wheat culture where it was most probable that there would be found original specific and varietal materials. Collections were made in all the basic regions where wheat is produced today, on all continents, and including both the older local varieties and new varieties produced by breeding. An important study of the local varieties of our regions was made by the Bureau of Applied Botany. Beginning in 1908, K. A. FLAKSBERGER carried out extensive investigations of local wheat materials of all our region, making an exhaustive study of the rich source of materials in agricultural exhibits, particularly the All-Russian Agricultural Exposition of 1923. An important role in the study of local wheats has been played by our breeding stations (Kharkov, Moskva, Saratov, Omsk, and others). As is known, all of our breeding work in the past had been based exclusively on local materials.

The colossal amount of materials collected by the Institute of Plant Industry within the limits of the Soviet Union and in foreign countries, totalling more than 31,000 samples with definite ecological-geographical data, was investigated by the method of differential systematics, including the use of cytology and genetics. In this way there developed a new botanical-geographical basis for understanding wheat.

The facts disclosed by the investigations exceeded all expectations. It was found that in this crop which has been studied more than any other, and to which have been dedicated a series of monographs and the works of botanists and agronomists for about 200 years, our knowledge of the initial and specific materials was but fragmentary.

The magnitude of discovery of species and varieties by the Soviet expeditions may be comprehended from the fact that the number of new species of wheat found was twice as great as that included in the latest world monograph of Professor PERCIVAL (1921) while the number of botanical varieties of wheat was almost four times greater than that reported by PERCIVAL. Whereas PERCIVAL's monograph describes 195 botanical varieties (in the sense of KÖRNICKE), at present we have identified 650 varieties.

In contrast with the old assumption of ALPHONSE DE CANDOLLE as to the probable origin of wheat in Mesopotamia, and the conclusion of the Australian geographical botanist SOLMS-LAUBACH that wheat originated in Central Asia, the problem of the origin of the important bread grain appears to be more complicated, but at the same time more concrete. All of the colossal diversity of wild and cultivated wheats can be classified into three groups according to the number of chromosomes specific for the different species, which are in a multiple series of 14-28-42 chromosomes (diploid number) or 7-14-21 (haploid number). This division is confirmed by all of the methods of present-day systematics, morphology, the results of crossing, physiological and anatomical



CENTERS OF THE ORIGIN
OF CULTIVATED SPECIES OF WHEAT WITH 28 CHROMOSOMES
Triticum durum subsp abyssinicum Vav
" turgidum subsp abyssinicum Vav
" polonicum subsp. abyssinicum Vav.
" dicoccum subsp. abyssinicum Steud.
" persicum Vav
" timopheevi Zhuk.
" orientale Perc.
" dicoccum europ. (Perc.) Vav.
" dicoccum asiaticum Stol.
Limit of northern culture of hard wheat
Tr durum subsp. expansum Vav
A sec. africana Vav
H gr. horanica Vav
gr. egyptiaca Vav
m sec. mediterranea Vav.
E sec. europaea Vav.
gr. eligulata Flaksb.
T Triticum turgidum subsp. mediterraneum Flaksb.
V Tr. polonicum mediter. Vav.

— FIGURE 10 —

peculiarities, sero-diagnostic reactions, geographical distribution, and ecological characteristics. This divison of the genus has cardinal importance for breeding.

All of the diverse wild and cultivated forms of wheat known today may be divided systematically into the following series of species:

Species and Subspecies of Cultivated and Wild Wheat:—

With 21 chromosomes:—

1. *Triticum vulgare* Vill. Soft wheats at present occupying a great area. The basic region of origin—southwestern Asia.

1a. *T. vulgare compositum* Tum. (*T. vavilovianum* Jakubz.) Endemic in Turkish Armenia.

2. *Triticum compactum* Host. Club wheat—southwestern Asia. Basic source of origin—Afghanistan and Armenia.
3. *T. sphaerococcum* Perc. Basic source of origin, northwestern India.
4. *T. spelta* L. Spelt. Basic source of development of varieties of this species—Asturias, southern mountains of Germany, Tyrol, and possibly northeastern Turkey (?).
5. *T. macha* Dekapr. and Men. Macha wheat. Endemic in western Georgia (SSSR).

With 14 chromosomes:—

T. durum Desf. (in sensu lato)

6. Subsp. *abyssinicum* Vav. *acutidenticulatum* Flaksb. Abyssinian hard wheat. Endemic in Abyssinia, Erithrea, and Yemen.
7. Subsp. *expansum* Vav. Occupies a broad area: Mediterranean region, southeast European part of SSSR, western Siberia, northwest region of USA. Basic source of formation—Mediterranean region including Asia minor.
8. *T. orientale* Perc. Cultivated occasionally in Iran, Turkey, Mesopotamia, and Central Asia.

T. turgidum L. (in sensu lato) English wheats:—

9. Subsp. *abyssinicum* Vav. Endemic in Abyssinia and Erithrea.
10. Subsp. *mediterraneum* Flaksb. English wheat. Basic source of formation of this species—region of southern Europe (Portugal, Spain, Italy, Balkans).

T. polonicum L. (in sensu lato) Polish wheat:—

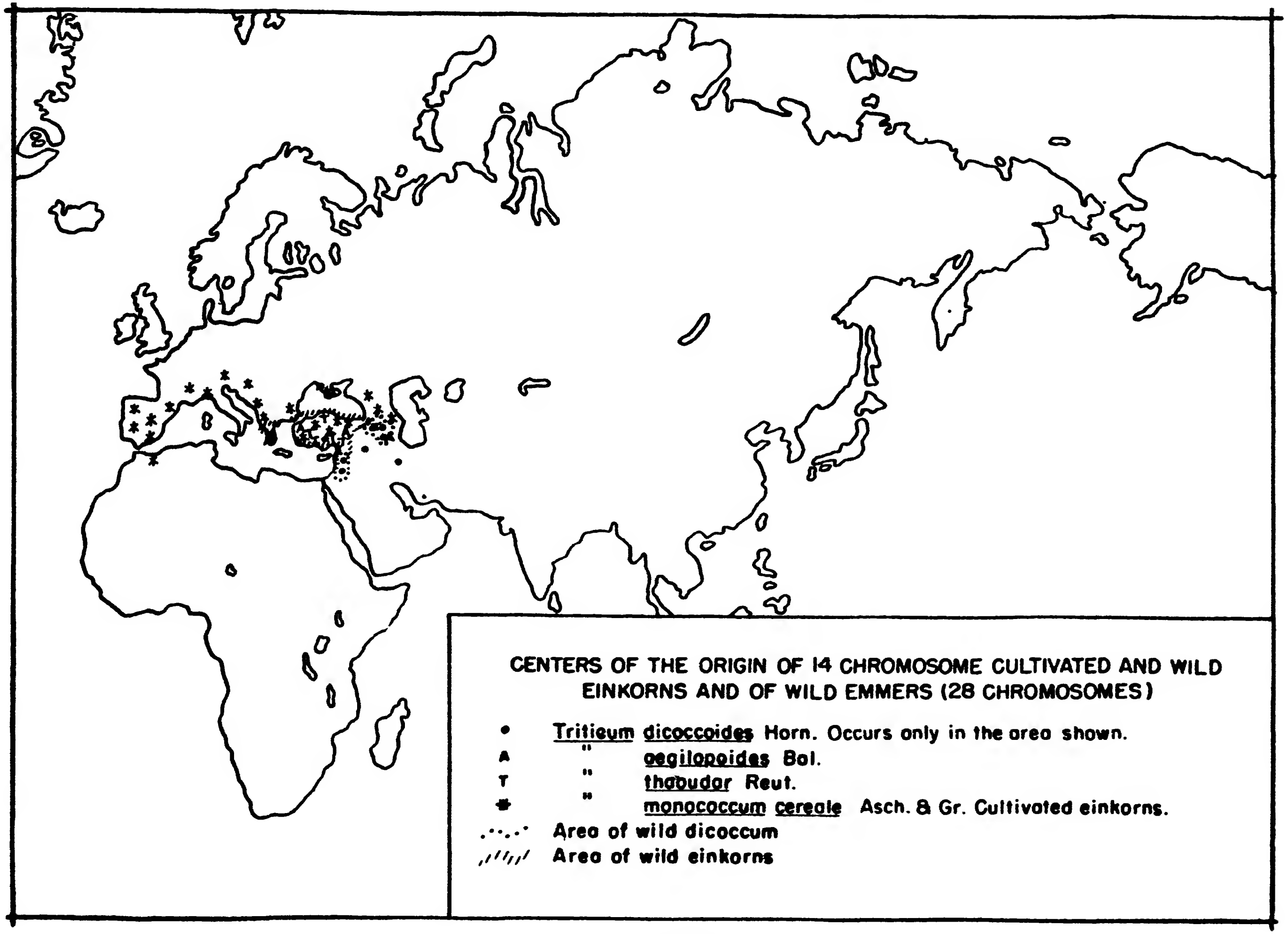
11. Subsp. *abyssinicum* Steud. Endemic in Abyssinia.
12. Subsp. *mediterraneum* Vav. Endemic in the region along the shores of the Mediterranean Sea.

T. dicoccum (Shrank.) Schubl. Emmer or 2-grained wheat:—

13. Subsp. *abyssinicum* Stoletova. Endemic in Abyssinia; also cultivated in Yemen and in India.
14. Subsp. *europeum* (Perc.) Vav. Cultivated in the mountainous regions of western Europe.
15. Subsp. *asiaticum* Stol. Endemic in Georgia, Armenia, northern Iran, and Central Asia.
16. *T. persicum* Vav.[60] Persian wheat. Endemic in the high mountainous regions of Dagestan, Georgia, Armenia, and northeastern Turkey.

[60] S. A. Nevski in the two volume "Flora of SSSR" (1934) has referred this species to *T. carthalicum* Nevski *i.e.*, to Carthalin wheat. Since one of the species of the genus *Aegilops*, called by Boissier *Aegilops persica*, was referred to by Aitchison and Hemsley (Trans. Linn. Soc., Ser. II, 3, 1886) under the name *Triticum persicum*, P. M. Zhukovski in his monograph of the genus *Aegilops* has called this species *Aegilops triuncialis* subsp. *persica* (Boiss.) Zhuk. Since the area occupied by Persian wheat includes not only little Carthaly, but all of Armenia, northeastern Turkey, Osset, and probably northern Iran, Nevski's conception can hardly be considered a fortunate one. Historically the subdivision of the species *T. persicum* is very instructive. It was first separated out from all the wheats in the World Collection, because of its unique immunity from powdery mildew, going under the name "Persian wheat," and referred by all botanists and breeders to *T. vulgare*. Later cytological and genetic study showed the distinctiveness of *T. persicum* from *T. vulgare*. In 1923 Professor P. M. Zhukovski described this in great detail as the independent species *T. persicum* Vav. (1919), cultivated in Trans-Caucasus. Later a number of investigators, including ourselves, found this species in great quantity (no less than 100,000 hectares) in Armenia, Georgia, and Osset. Individual heads of it were found in Iran; in recent years Persian wheat has also been found in N. E. Turkey. This species thus has wide distribution and includes many subspecies and races. Its greatest variation has been found in the mountains of Kakhetia.

Quite without justification, in our opinion, is the liquidation by S. A. Nevski of the species *T. dicoccum*, and also the assignment of *T. vulgare* Vill. to *T. aestivum* L.—spring wheat, since within this species are found not only spring forms, but also winter ones. Along with *T. dicoccum* he separates out the species *T. volgense* Nevski and *T. armeniacum* Nevski, *i.e.*, geographic races are considered species. If we followed Nevski, we would have to divide *T. aestivum* into dozens of species. We consider that the new classification of Nevski, or, more exactly, his name-changing, is not suitable for either botanical or breeding purposes.


CENTERS OF THE ORIGIN OF 14 CHROMOSOME CULTIVATED AND WILD EINKORNS AND OF WILD EMMERS (28 CHROMOSOMES)
• Triticum dicoccoides Horn. Occurs only in the area shown.
A " aegilopoides Bal.
T " thaoudar Reut.
* " monococcum cereale Asch. & Gr. Cultivated einkorns.
Area of wild dicoccum
Area of wild einkorns

— FIGURE 11 —

17. *T. dicoccoides* Körn. (wild forms). Wild emmer. Basic area: southern Armenia, northeastern Turkey, western Iran, Syria, and northern Palestine. Genetically this is somewhat distinct from the cultivated 28-chromosome wheats since it is partly sterile in crosses with them.
18. *T. timopheevi* Zhuk. Endemic in western Georgia. Genetically distinct from the preceding species as shown by the high degree of sterility of its hybrids. 7 of its chromosomes are not homologous with chromosomes of the preceding species.

With 7 chromosomes:—

19. *T. monococcum* L. Cultivated einkorn. Basic source of variation, the mountains of Karabakh, western Georgia, and northeastern Turkey.
20. *T. aegilopoides* Balan. (in sensu lato). Wild einkorn. Basic source—southern Armenia, Turkey, Georgia.

The total number of species and subspecies of wheat determined up to the present is twenty.

In the 21-chromosome group, along with the species that were distinguished long ago, *T. vulgare, T. compactum,* and *T. spelta,* PERCIVAL in 1921 separated out the species *T. sphaerococcum,* the low-growing shot wheat with characteristic coarse short leaves. This species is basically adapted to northwestern India. The specific morphology of the species and its adaptation to a limited region permit us to consider it as an independent systematic group. L. L. DEKAPRELEVICH found, in regions adjoining lower Svanetii, the species *T. macha* with glumes reminding one of *T. dicoccum,* but having 21 chromosomes. This species consists of winter wheat forms.

M. G. TUMANYAN, in specimens obtained from the region of Turkish Armenia, found an unusual branched 21-chromosome wheat, which differed in its difficult milling and large heads. The morphological features of this wheat, its xerophilic character, and its adaptation to certain ancient regions of culture, led M. M. YAKUBTSINER to separate it out, although not entirely convincingly, into the independent species named *T. vavilovianum.* There is no doubt that this group of forms is very unusual, and deserves special genetic study.

Thus the 21-chromosome group of wheats embraces five species, if we do not consider the distinct group of squareheads which practically may be separated out into an independent group (*T. capitatum*) as has been done by a number of systematists. The species *T. spelta, T. macha,* and *T. sphaerococcum* with comparatively few varieties, appear to be relicts of forms which have survived only in isolated, mountainous regions. Nevertheless they are very interesting to the breeder since they are distinguished by specific morphological and physiological characters, their limited soil requirements, their failure to shatter, their xerophilic habit, and their simple straw. *T. sphaerococcum* has remarkably large grain.

The greatest number of wheat species belong to the group with 14 chromosomes. First of all among the hard wheats (*T. durum*), regarding this species in a broad sense, it is necessary to separate out two distinct subspecies, namely, the subspecies of Abyssinian hard wheat and the group of ordinary hard wheats of the "Kubanka" type. The first of these we call *T. durum* subsp. *abyssinicum,* the second *T. durum,* subsp. *expansum,* as it occupies a wide area.

The complex of ecological and physiological characters which distinguishes these two groups is so marked that there is no doubt about their clear-cut distinction into two subspecies, or even into independent species. Each of these subspecies contains a great number of different varieties, hundreds of botanical forms. The Abyssinian hard wheats are distinguished from our ordinary hard wheats by their early maturity, low growth, hairy leaves, and comparative susceptibility to rust; in their diversity they also include endemic forms such as the violet-grained wheats, and the awnless hard wheats.

In the same manner we divide *T. turgidum* into two subspecies. The typical Mediterranean forms of English wheat (*T. turgidum mediterraneum*) are distinguished by their high productivity, late ripening, tall growth, large leaves, and resistance to rust. These are giants in comparison with the Abyssinian *T. turgidum abyssinicum*. Ecologically, and according to vegetative characters, the Abyssinian *T. turgidum* is very close to the Abyssinian *T. durum*, representing a group of inflated hard Abyssinian wheats.

The Polish wheats, *T. polonicum*, are also divided into groups.

T. dicoccum is strikingly differentiated into ecological-geographical types.

The western European emmers are distinguished by a high degree of resistance to powdery mildew and to different rust species. On the other hand, the Asiatic forms of emmers are very susceptible to these fungi. The western European forms are distinguished by their late ripening. They include some winter forms. On the contrary, the Abyssinian forms are distinguished by early maturity. There are also marked differences in vegetative characters.

T. persicum has a large diversity of forms and is no doubt a good botanical species adapted to a definite ecological habitat in the high mountainous regions of Caucasus, particularly in Trans-Caucasus, being characterized physiologically by its ability to grow at low temperatures. On the whole this species is distinguished by its high degree of resistance to powdery mildew, and also to species of rust, including stem rust.[61]

Triticum persicum, as we have shown (1925), is easily crossed with all the species of 28-chromosome wheats (*T. durum, T. dicoccum, T. polonicum, T. turgidum*) giving entirely fertile hybrids.

T. orientale, which was separated out by PERCIVAL, inhabits a very limited area not extending beyond the limits of Near and Central Asia (Turkey, Iran, and Kazakstan). This species, which has little adaptation to differences in environmental conditions, is comparatively more heavily attacked by rust than *T. durum* subsp. *expansum*. Its long, vitreous grain resembles that of Polish wheat, and according to head characters it occupies a position intermediate between Polish and hard wheat.

T. polonicum is associated with *T. durum* subsp. *expansum* and subsp. *abyssinicum;* it does not have a well-defined area; it is encountered in northern Africa, Syria, Palestine, and in Abyssinia, and it has ecological features corresponding to a geographical group of hard wheats.

All the numerous species of 28-chromosome cultivated wheats are easily crossed with one another, and produce entirely fertile hybrids.

The new species of wheat, *T. timopheevi*, with 14 chromosomes, which was recently discovered by P. M. ZHUKOVSKI in western Georgia, deserves particular attention of the breeder. This species is distinguished from all the 21-14 chromosome wheats by its striking resistance to all species of rust, to smut, and to powdery mildew. It is also entirely resistant to the Swedish and Hessian fly. According to the artificial inoculation experiments of DICKSON (U.S.A.), this species is also resistant to fusariose. Genetically it is distinct from the other 14-chromosome wheats by showing considerable sterility in crossing with them.

The cultivated einkorns (7 chromosomes) also show a great diversity of forms. All of the einkorns are characterized by their high resistance to attack of rust, powdery mildew, and smut. This group is quite distinct both in its number of chromosomes and in the difficulty in using it in crosses. The einkorns cross with more difficulty either with hard or with soft wheats than

[61] N. I. VAVILOV and O. V. YAKUSHKINA. [On the phylogeny of wheat. Hybridological analysis of the species *Tr. persicum*.] Trudi po Prikl. Bot. 15 (1925).

the latter with each other. Nevertheless this species, to a definite extent, may be used in breeding programs.

Intraspecific Constitution of Wheat:— The botanical-differential method of study which we have worked out on wheat,[62] has been used in discriminating a great number of morphological and physiological characters which distinguish hereditary forms within the limits of wheat species. Each of these characters, in turn, may be subdivided according to differences in expression of the character (different intensities of color, differences in length of awns, etc.). In addition we must consider the necessity of studying anatomical, physiological, and biochemical variety differences.

Finally the different characters are subject to changes due to the environment. Marked changes in conditions, for example those induced by vernalization, may call forth changes in a number of characters, including morphological differences as in awnedness and color of the head.

The extensive investigations of materials collected from the original home of the plant have brought to light striking heritable differences in forms of the wheat already existing in nature. In 1920 at the Breeding Conference in Saratov, when we first attempted to point out the variation in soft wheat, we spoke of the existence of several thousand heritable forms of wheat, whereas, at the present time we would not attempt to suggest the statistical number of heritable forms of wheat in nature, considering the great number of combinations of more than 400 characters that might exist. In any case, it would run into the millions, not considering those variations which may be obtained as a result of artificial crossing of the different species.

Conventionally, for orientation among the diversity of wheats within the limits of species, present day systematists use the most easily distinguished head and grain characters. At the present time we must consider as artificial KÖRNICKE's morphological subdivision of species into botanical subspecies, based principally on the characters of awnedness, color of grain, hairiness of the glumes, and color of the heads. Yet, with all its defects, in the sense of combining within single subspecies forms that have fundamental ecological-geographical and even morphological differences, this classification still has much practical use and it is constantly employed in the first survey of varied forms.

At the present time, among all the species of wheat, there have been determined about 650 of such botanical subspecies. We need to bear in mind that some of the subspecies of KÖRNICKE consist of great numbers of forms distinguished by dozens of clear-cut morphological and biological characters. Some subspecies of soft wheats (for example, *lutescens, erythrospermum, ferrugineum, albidum,* and others) contain literally thousands of hereditary forms.

Such a great amount of differentiation calls for new principles in classification. It appears to be particularly important to have an ecological-geographical classification, divided into natural categories of biotypes adapted to definite environmental conditions. Below we have given a scheme of the variations within wheat species characterized by 21, 14, and 7 chromosomes, which clearly illustrate the amplitude of hereditary variation with which the breeder must work.

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[62] N. I. VAVILOV. [On soft wheats.] Trudi po Prikl. Bot. 13 (1923).

Scheme of Hereditary Variation of Characters in Species of Wheat[1]:—

HEAD CHARACTERS

CHARACTER	SUBDIVISION	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
1. Awnedness	A. Awned	+++[2]	+++	+++
	B. Short awned	+	+	+
	C. Semi-awned (awns only on the upper half of the head)	+	+	+
	D. Awnless with awnlike projections on the upper part of the head	+++	+	..
	E. Entirely awnless	+	..	..
	F. With deformed awns (*inflatum*) and inflated glumes	+	+	..
	G. An extreme degree of deformation of the awns (furcate)	+	+	..
2. Compactness	A. Loose	+++	+++	+
	B. Moderately compact	+++	+++	+++
	C. Compact	++	++	++
3. Color of the mature head	A. White (straw yellow)	+++	+++	+++
	B. Light red	+++	+++	++
	C. Dark red	++	+	++
	D. Coffee brown	+	+	+
	E. Black with white background	+	+	+
	F. Black with red background	+	++	++
	G. Brownish gray	+	+	+
4. Color of head before ripening	A. Light green	+++	+++	+++
	B. Dark green	+++	+++	+
	C. Violet	..	+	..
5. Hairiness of glumes	A. Smooth	+++	+++	+++
	B. Tuberculate	+	+	++
	C. Hairy	+++	+++	+++
	D. Weakly pubescent	+	+	++
	E. Strongly pubescent	+	+	++
6. Form of the head	A. Spindle-shaped	+++	+	+
	B. Cylindrical	+++	++	..
	C. Erect	..	+	+
	D. Nodding	+	+	+
7. Transverse section of head	A. Square	++	++	..
	B. Rectangular	+++	+++	+++
	C. Nearly circular	+++	+++	..
	D. Trapezoidal	..	..	+++
8. Length of head	A. Short	++	++	+
	B. Long	++	++	+++
	C. Medium	+++	+++	+++
9. Waxy layer on head after ripening	A. Absent	+	++	+++
	B. Disappearing	+++	+++	..
	C. Persistent	+	+	..
10. Number of spikelets in a head	A. Many	++	++	++
	B. Few	++	++	+++
11. Color of glume margins	A. With black margins	+	++	++
	B. Without black margins	+++	+++	+++
12. Form of glumes	A. Oval	+++	+	..
	B. Boat-shaped	+++	+++	..
	C. Wide rhomboidal	+	..	..
	D. Long lance-shaped	..	+	+++
	E. Strongly convex	++	++	..
	F. Weakly convex	+++	+++	+++

[1] Prepared by M. M. YAKUBTSINER from our data, and supplemented by us.

[2] +++ = the character widely distributed.
++ = the character comparatively frequent.
+ = the character infrequent.

Hereditary Variation of Characters in Wheat (*continued*) :—

Character	Subdivision	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
13. Form of glume shoulder	A. Almost lacking	+	+	+++
	B. Bevelled	+++	+++	..
	C. Raised	++	++	..
	D. Round	++	++	..
	E. Almost straight	+	+	..
14. Length of glume	A. Short	++	++	+
	B. Long	+	++	++
	C. Medium	+++	+++	+++
	D. Extremely long (*polonicum* type)	..	++	..
15 Width of glume	A Narrow	+++	++	+++
	B. Wide	++	+++	..
16. Consistency of glume	A. Ordinary	+++	+++	+++
	B. Papery (*polonicum* type)	..	+	..
17. Character of glumes	A. Fine (*tenerum*)	+	+	++
	B. Coarse (*rigidum*)	+	++	+++
	C. Intermediate	+++	+++	+++
18. Form of keel teeth	A Sharp	+++	++	+++
	B Blunt	+++	+++	+
19 Color of keel teeth	A Black	+	+	+
	B Color of the glume	+++	+++	+++
20. Orientation of keel teeth	A. Straight	+	+	+++
	B. Pointed inward	+++	+++	..
	C. Club-like	+	+	..
	D. Curved out	+	++	..
21. Length of keel teeth	A. Barely expressed	++	++	++
	B. Short	+	+++	++
	C. Long	+++	++	..
	D. Tooth-awn	+	++	..
	E. Longer at the top of the head	++	++	++
	F. Shorter at the top of the head	..	+	..
	G. Equal throughout the head	++	++	+++
	H. Varying irregularly according to dimensions of the head	+	+	..
22. Development of the keel	A. The entire length of the glume.	+	+++	+++
	B. Not reaching to the base of the glume	+++	+	..
	C. Absent	..	+	+
23. Size of the keel	A. Wide	+	+++	+
	B. Narrow	+++	+	+++
24. Presence of teeth on the keel	A. Teeth along its entire length	++	++	+++
	B. Teeth in upper part	+++	+++	+
	C. Almost no teeth	+	+	..
	D. Short teeth	+++	+++	+
	E. Long teeth	+	+	+++
	F. Few teeth	+++	+++	+
	G. Abundant teeth	+	+	+++
25. Nervature of the glumes	A. Many nerves	+++	+++	+++
	B. Few nerves	+	+	+
26. Dentation of keel teeth	A. Strongly dentate	++	+++	+++
	B. Weakly dentate	++	++	+
27. Length of awns	A. Long	..	+++	+++
	B. Short	++	+	+
	C. Intermediate	+++	+++	..
28. Orientation of awns	A. Extending out from head	+++	+	+
	B. Parallel to head	+	+++	+++
29. Character of awns	A. Coarse	++	++	+++
	B. Fine	++	++	+
	C. Falling at maturity	..	++	..
	D. Not falling	++	+++	+++

HEREDITARY VARIATION OF CHARACTERS IN WHEAT (*continued*) :—

	Character	Subdivision	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
	30. Straightness of awns	A. Straight	+++	+++	+++
		B. Bent like a bayonet	+	+	..
		C. Weakly curved	++	+	+
	31. Color of awns	A. White (straw-yellow)	+++	+++	+++
		B. Red (cinnamon-brown)	+++	+++	+++
		C. Black (dark gray)	+++	+++	+
		D. Only the teeth on the awns black	+	+	..
	32. Dentation of awns	A. Awns almost smooth	..	+	..
		B. Slightly roughened	..	+	..
		C. Strongly toothed	+	+	..
		D. Moderately toothed	+++	+++	+++
	33. Number of florets in a spikelet	A. Few	++	++	+++
		B. Many	+++	+++	..
	34. Number of grains in a spikelet	A. Many	+++	++	..
		B. Few	++	++	+++
	35. Length of spikelets	A. Short	+++	+	+
		B. Long	+	++	+++
		C. Medium	++	+++	++
	36. Width of spikelets	A. Narrow	++	++	+++
		B. Wide	+	+	..
		C. Medium	++	+++	+
HEAD CHARACTERS	37. Branching of rachis	A. Simple	+++	+++	+++
		B. Branched	+	++	..
		C. With double spikelets	+	+	..
	38. Degree of branching	A. Branching throughout almost entire length	+	..	..
		B. Branching in lower half	..	+	..
		C. Branches forming secondary heads (*turgidum* type)	..	+	..
		D. Branches not forming secondary heads (*compositum* type)	+	+	..
	39. Hairiness of rachis	A. Very hairy	..	++	+++
		B. Slightly hairy	+++	++	++
		C. Intermediate	+++	+++	++
		D. With long hairs	..	+	++
		E. With short hairs	++	++	++
		F. Only at spikelet base	+	+	+
		G. At sides and base	++	++	++
		H. Hairy at nodes and internodes	..	+	++
	40. Brittleness of rachis	A. Brittle	+	++	+++
		B. Falling to pieces	..	+	+++
		C. Not brittle	+++	+++	..
	41. Length of internodes of rachis	A. Long	+++	+++	++
		B. Short	+++	++	++
		C. Intermediate	+++	+++	+++
	42. Width of inter nodes of rachis	A. Wide	+++	+++	+++
		B. Narrow	..	+	..
		C. Intermediate	+++	+++	+++
	43. Form of internodes of rachis	A. Straight	+++	+++	++
		B. Somewhat curved	+	+	+
		C. Wedge-shaped	+	..	..
CHARACTER OF GRAIN	44. Color of grain	A. White (yellow)	+++	+++	+
		B. Light red	+++	+++	+++
		C. Dark red	++	++	+
		D. Violet	..	++	..
		E. Green	+	..	+

HEREDITARY VARIATION OF CHARACTERS IN WHEAT (*continued*) :—

CHARACTER OF GRAIN

	CHARACTER	SUBDIVISION	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
45.	Form of grain	A. Spherical-ovoid	+++	+++	..
		B. Long-oval	+++	+++	+
		C. Curved	++	++	..
		D Crescent-shaped	..	+	..
		E. Flat, laterally compressed	..	+++	+
46	Cross section	A. Circular	++	++	..
		B. Angular	+	+	+
		C. Lens-shaped	..	..	+++
47.	Length of grain	A. Short	+++	++	+
		B. Long	++	+++	+
		C. Intermediate	+++	+++	+++
		D. Very long (*polonicum* type)	..	++	..
48.	Width of grain	A Narrow	++	++	+++
		B Wide	++	++	+++
		C Intermediate	+++	+++	+
49.	Wrinkling of grain	A. Absent	+++	+++	+++
		B. Present	..	+	..
50.	Consistency of grain	A. Vitreous	..	..	..
		B. Semi-vitreous	++	+++	+
		C. Mealy	+++	++	..
		D. Waxy	..	+	..
51.	Grain crease	A Small	++	++	+
		B Deep	++	++	++
		C. Wide	++	++	+
		D. Narrow	++	++	++
52.	Hairiness of the grain apex	A. Long hairs	+++	+	++
		B. Short hairs	+	+++	++
		C. Abundant hairs	..	+	+
		D. Few hairs	+++	+++	+++
		E. Almost hairless	+	+	..
53.	Embryo of grain	A. Convex	++	++	++
		B Concave	++	++	++
		C. Round	++	++	+
		D. Elongated	++	++	++
54.	Chemical composition of grain	A. Rich in protein	++	++	++
		B. With little protein	++	++	+
		C. Intermediate	++	++	++
55.	Absolute weight	A. Low	+	..	+++
		B. High	+	++	+
		C. Intermediate	+++	+++	+++
		D Extremely high (weight per 1000 grains 60-80 grams) (*polonicum* type)	..	+	..
56.	Nature of grain	A High	++	++	+
		B. Low	++	++	+
		C. Intermediate	+++	+++	+++
57.	Water-absorptive power	A. Strong	+++	+++	..
		B. Weak	+++	+++	..
		C. Intermediate	+++	+++	++
58.	Milling	A. Difficult	++	++	+++
		B. Easy	++	++	..
		C. Intermediate	+++	+++	+
59.	Flour yield	A. High	++	++	..
		B. Low	++	++	+
		C. Intermediate	+++	+++	+
60.	Crumbiness of bread	A. Great	++	++	+
		B. Little	++	++	..
		C. Intermediate	+++	+++	+
61.	Porosity of the bread	A. Coarse	++	++	..
		B. Fine	++	++	+
		C. Intermediate	++	+	+

HEREDITARY VARIATION OF CHARACTERS IN WHEAT (*continued*) :—

VEGETATIVE CHARACTERS

CHARACTER	SUBDIVISION	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
62. Leaf structure	A. ligulatum—with a well developed ligule	+++	+++	+++
	B. eligulatum—without a ligule	. +	+	..
	C. With a reduced ligule	+	+	..
63. Form of the plant	A. Erect	+++	+++	+
	B. Trailing	++	++	+++
	C. Semi-trailing	++	++	+++
	D. *prostratum* type	..	++	++
64. Number of vascular bundles in coleoptile	A. Two	+++	+++	+++
	B. Several	..	+	..
65. Color of coleoptile	A. Violet	+	++	+++
	B. Green	+++	+++	+
66. Hairiness of seedling	A. Smooth	+	+++	..
	B. Short-haired	+++	++	..
	C. Intermediate	+++	+	++
	D. Velvety	++	++	++
	E. Woolly	+	..	..
	F. Ciliate	+	+	..
67. Hairiness of the leaf sheath	A. Smooth	+	+++	..
	B. Short-haired	+++	++	+
	C. Velvety	++	++	..
	D. Woolly	+	..	..
	E. Ciliate	+	+	++
68. Hairiness of the edge of the leaf sheath	A. Without hairs	+++	+++	+
	B. With hairs	+	+	+++
69. Hairiness of the leaf blade	A. Smooth	+	+++	..
	B. Short-haired	+++	++	..
	C. Velvety	++	++	++
	D. Woolly	+	..	..
	E. Ciliate	..	+	+++
70. Hairiness of border of leaf blade	A. Without hairs	+++	+++	+
	B. Hairy	+	+	+++
71. Length of leaf blade	A. Short	++	++	..
	B. Long	++	+++	+
	C. Intermediate	+++	+++	+++
	D. Extremely long	..	+	..
72. Width of leaf blade	A. Narrow	++	++	+++
	B. Wide	++	+++	..
	C. Intermediate	+++	+++	++
73. Color of leaf	A. Light green	+++	+++	++
	B. Dark green	+++	+++	+++
74. Number of stomata of leaf	A. Large	+	+++	+++
	B. Small	+++	++	..
	C. Intermediate	+++	++	..
75. Size of stomatal cells on leaf	A. Large	+++	++	..
	B. Small	++	++	+++
	C. Intermediate	+++	+++	++
76. Drooping of leaf	A. Slightly drooping	+	+	+
	B. Strongly drooping	++	++	+++
	C. Almost no drooping	+	..	..
77. Character of leaf	A. Coarse	+++	+++	+++
	B. Fine	+++	+++	+
78. Leafiness	A. Weak	+	+	+
	B. Strong	+	++	+++
	C. Intermediate	+++	+++	++
79. Waxy layer on leaf and stem	A. Weak	+++	+++	+++
	B. Strong	+++	+++	..
	C. Intermediate	+++	+++	..
	D. Absent	+	++	+++

HEREDITARY VARIATION OF CHARACTERS IN WHEAT (*continued*) :—

VEGETATIVE CHARACTERS

	CHARACTER	SUBDIVISION	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
80.	Form of ligule	A. Bordered	+++	+++	+++
		B. Tapered	+	+	+
81.	Size of ligule	A. Short	++	++	++
		B. Long	++	++	+
		C. Intermediate	+++	+++	++
82	Color of ligule	A. Violet	..	+	+
		B. Colorless	+++	+++	+++
83.	Presence of auricula	A. Present	+++	+++	+++
		B. Absent	+	+	..
		C. Rudimentary	+	+	..
84.	Size of auricula	A. Short	+++	+++	++
		B. Long	+++	+++	++
		C. Intermediate	+++	+++	++
85	Color of auricula	A. Violet	+	++	+++
		B. Colorless	+++	+++	+
86	Color of stem at maturity	A. Violet	++	++	+++
		B. Green	+++	+++	+++
87	Color of stem after maturity	A. Violet	+	+	+
		B. Yellow	+++	+++	+++
88.	Length of lower internode	A. Short	++	++	+++
		B. Long	++	++	+
		C. Intermediate	+++	+++	+
89.	Form of nodes	A. Very convex	+	++	+
		B. Weakly convex	++	++	+
		C. Intermediate	+++	+++	++
90.	Length of nodes	A. Short	+++	++	++
		B. Long	++	+++	++
		C. Intermediate	+++	+++	++
		D. Extremely long	..	+	.
91	Color of nodes	A. Green	+++	+++	..
		B. Violet	+	++	+++
92	Hairiness of nodes	A. Smooth	++	++	..
		B. Weakly hairy	+++	+++	+
		C. Very hairy	+	++	+++
93.	Number of nodes on principal stem	A. Small	+	+	+
		B. Large	++	++	+
		C. Intermediate	+++	+++	+++
94.	Height of plant	A. Low-growing	++	++	+
		B. Average height	+++	++	++
		C. Tall	++	++	+++
		D. Dwarf forms	+	+	..
		E. Extremely tall	..	+	..
95.	Thickness of straw	A. Thin	++	+	+++
		B. Thick	+	++	..
		C. Average thickness	+	+	+
96.	Straw walls	A. Thin	+++	+++	++
		B. Thick	+++	+++	..
97.	Solidness of straw under the heads	A. Hollow	+++	+	+
		B. With small aperture	+	+++	+++
		C. Solid	..	+++	++
98.	Hairiness of straw under the head	A. Smooth	+++	+++	+++
		B. Hairy	+	..	..
99.	Straw under the head	A. Straight	+++	+++	+++
		B. Curved	+	+	+
100.	Position of head	A. Sharply inclined	++	++	+
		B. Almost vertical	++	++	+++
		C. Nodding	..	+	..

HEREDITARY VARIATION OF CHARACTERS IN WHEAT (*continued*) :—

	CHARACTER	SUBDIVISION	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
VEGETATIVE CHARACTERS	101. Tillering	A. Weak	+++	+++	+
		B. Strong	+++	+++	+++
		C. Intermediate	+++	+++	++
	102. Color of pollen	A. Yellow	+++	+++	++
		B. Violet	+	++	++
	103. Size of pollen	A. Long	+	+	+++
		B. Short	+++	+++	+
PHYSIOLOGICAL CHARACTERS	104. Life habit (under definite field conditions)	A. Spring type	+++	+++	+++
		B. Winter type	+++	++	+++
		C. Semi-winter type	++	++	+
	105. Energy of germination	A. Seedlings developing rapidly	+++	+++	++
		B. Seedlings developing slowly	+++	+++	+
	106. Varietal differences in reaction in early stages to temperature effect (vernalization stage)	Varieties differing in reaction to different temperatures and the duration of their effects, essential for hastening development. Varieties may be subdivided into several groups	+++	+++	+++
	107. Varietal differences in light requirements (duration of illumination) for accelerating development in the second stage of growth	Varietal differences in light requirements (different number of hours)	+++	+++	+++
	108. Earliness of maturity under given environmental conditions	A. Heading early	+++	+++	++
		B. Heading late	+++	+++	+++
		C. Intermediate heading	+++	+++	+
		D. Early ripening	+++	+++	++
		E. Late ripening	+++	+++	+++
		F. Intermediate ripening	+++	+++	+
	109. Blossoming	A. Open	+	++	+
		B. Closed	+++	+++	+++
		Relation to fungus parasites			
BIOLOGICAL CHARACTERS	110. To stripe rust (*Puccinia glumarum*)	A. Resistant	++	+++	+++
		B. Susceptible	+++	+	..
		C. Intermediate	+++	+	..
	111. To leaf rust (*Puccinia triticina*)	A. Resistant	+	+++	+++
		B. Susceptible	+++	+	..
		C. Intermediate	++	+	..
	112. To stem rust (*Puccinia graminis*)	A. Resistant	+	++	+++
		B. Susceptible	+++	++	..
		C. Intermediate	+++	++	+
	113. To powdery mildew (*Erysiphe graminis*)	A. Resistant	..	++	+++
		B. Susceptible	+++	++	..
		C. Intermediate	+	++	..
	114. To fusariose (*Fusarium roseum*)	A. Resistant	+	++	++
		B. Susceptible	++	+	+
		C. Intermediate	+	+	+
	115. To bunt (*Tilletia tritici* and *T. levis*)	A. Resistant	+	+	++
		B. Susceptible	+++	+++	..
		C. Intermediate	+++	+++	+
	116. To loose smut (*Ustilago tritici*)	A. Resistant	+	++	++
		B. Susceptible	+++	+	..
		C. Intermediate	+++	++	+

Hereditary Variation of Characters in Wheat (*concluded*) :—

Biological characters

Character	Subdivision	Species with 42 chromosomes (2n) *T. vulgare* and others	Species with 28 chromosomes (2n) *T. durum* and others	Species with 14 chromosomes (2n) *T. monococcum* and others
	Degree of attack by insects			
117. Swedish fly	A. Strongly attacked	+++	+++	+
	B. Weakly attacked	+	+	++
118. Hessian fly	A. Strongly attacked	+++	+++	..
	B. Weakly attacked	+	+	++
	Cold- (freeze-) resistance			
119. To low temperatures in the seedling stage	A. Strongly resistant	++	+	..
	B. Weakly resistant	+++	+++	++
	C. Intermediate	+++	++	++
120. To low temperatures in the second stage of development (boot stage)	A. Resistant	+++	+	+
	B Weakly resistant	+	+++	++
	C. Intermediate	++	++	++
	Drought resistance			
121. To soil dryness	A. Strongly resistant	++	++	+
	B. Weakly resistant	+++	+++	++
	C. Intermediate	++	++	+
122. To dry air in the early stage of growth (up to heading)	A. Strongly resistant	++	++	+
	B. Weakly resistant	+++	+++	++
	C. Intermediate	++	++	+
123. To dry air in the second period of growth	A Strongly resistant	++	++	+
	B. Weakly resistant	+++	++	++
	C. Intermediate	++	++	+
	Other biological characters			
124. Heat resistance	A. Strongly resistant	++	++	+
	B. Weakly resistant	+++	+++	+++
	C. Intermediate	++	+	+
125. Resistance to excessive water	A. Resistant	+	+	..
	B Weakly resistant	+++	+++	++
126. Resistance to lodging	A. Strongly resistant	++	++	+++
	B. Weakly resistant	+++	+++	+
	C. Intermediate	+++	+++	+++
127. Fertilizer requirement	A. With small fertilizer requirement	+++	+++	+++
	B. Very sensitive to fertilization as shown by increased yields ..	+++	+++	..
128. Shattering of the grain at maturity	A. Varieties inclined to shatter ..	+	+	++
	B. Non-shattering	+++	+++	++
129. Tendency to cross-pollination	A. Natural tendency to cross-pollination	+	+	..
	B. Very little of such tendency ..	+++	+++	+++

Trans-Caucasian Center of Cultivated and Wild Wheats:— In addition to Abyssinia, a great diversity of species and forms of 14-chromosome wheats is concentrated in Trans-Caucasus and along the shores of the Mediterranean Sea. Recent investigations have shown the development of the formative process within the limits of Georgia and Armenia. Here have been found endemic species such as *T. persicum, T. timopheevi,* and *T. macha.* The first of these occupies a comparatively wide area comprising the high-mountainous region of Armenia and Georgia and ascending to the north to Osset and Erzerum in Turkey. According to our approximate estimation no less than 100,000 hec-

tares are occupied by it. The species *T. timopheevi* and *T. macha* are very narrowly localized, and despite careful searches they have been found only in very limited quantity (on areas totalling less than 300-400 hectares) in regions adjacent to lower Svanetii, to the north of Kugan. It is possible that both *T. macha* and *T. timopheevi* existed earlier in northeastern Turkey; they are cultivated in Georgia in forest strips on cleared lands, and no doubt have been brought in here, although probably long ago.

The hard wheats of Azerbaidzhan and Georgia are very rich in forms; this is particularly true of forms of dwarf soft wheats, emmers, and hard wheats in little Armenia. Trans-Caucasia, along with the Mediterranean region and Abyssinia, is no doubt a very important source of species- and variety- formation of the 14-chromosome wheats, and deserves particular attention with respect to immunity from diseases.

The emmers are particularly distributed at the present time in Armenia, the Tatar Republic, the Chuvash Republic, the Pyrenees and Basque area, Abyssinia, Eritria, small areas in the mountains of Italy, the Balkans, and the mountains of Morocco.

The third group of wheats, the einkorns, having a haploid number of 7 chromosomes, are concentrated with their fundamental potentialities in Trans-Caucasus, particularly in the foothills of Karabakh, and in Asia Minor. The foothill region of Karabakh in the southern part at the present time is evidently an area of concentration of the most varied forms of cultivated einkorns, which here appear to be mixed with emmers.

The wild einkorns are widely distributed in the mountains of Armenia, particularly in the region adjacent to Mt. Ararat where they display a great diversity of forms, and grow as weeds along with emmers and different species of *Aegilops* and *Secale vavilovi* Grossh.—annual wild rye. Within the limits of Armenia, near Erivan, there may now be seen wild relatives of wheat in great quantity; here is concentrated a striking diversity of cultivated subspecies of wheat including endemic species, such as *T. persicum;* here are cultivated many varieties of *T. compactum* and emmers are widely grown.

Within the limits of Trans-Caucasus the species-formative process has been most active, by a doubling of the chromosome complex which is made possible by the temperature conditions of mountainous regions.[63] Armenia, within the limits of Soviet Trans-Caucasus, is particularly rich in species and subspecies of various cultivated and wild wheats. Professor M. G. TUMANYAN found here some 250 botanical varieties of cultivated and wild wheats.[64] The number of varieties of wheat in Armenia is greater than that in all of the other Russian areas put together. *Triticum persicum* and its varieties are concentrated principally in the mountains of Georgia, on the southern slope of the main Caucasus range, where dominant forms are found (black-headed forms, hairy forms, etc.)

The geographic localization of wheat variants appears to be basic in the study of initial materials for wheat breeding. We have only begun in recent years to grasp the full significance of this fact. It leads investigators in a concrete fashion to a mastery of wheat. The basic fact of capital significance for breeding in the present and the future—the great natural potential of species

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[63] We have gathered near Erivan a number of wild einkorns (7 chromosomes) and emmers (14 chromosomes) which, according to their morphological characters were strikingly similar. The emmers differed principally in their gigantism. A similar thing has been noted by us in the mountains of Caucasus for a number of other wild plant species. These facts deserve further investigation.

[64] M. G. TUMANYAN. [Identification of cereals.] Erivan, 1933.

and variety diversity, has been entirely unrecognized in the past. If this point has been ascertained for wheat, we may judge how little we know of the initial materials of other cultivated plants.

Amplitude of Variations in Soft and Hard Wheats:— The wealth of new species and varietal materials in wheat disclosed by our investigations leads us to a new basis for procedure. Despite the opinion of the predominance of variation in soft wheats, held by PERCIVAL and other workers, our investigation of the 28-chromosome wheats has disclosed a very wide amplitude of heritable variation in these, exceeding the variability in soft wheats. In grain size, grain color, head size, glumes, plant height, leaf dimensions, length of awns, vegetative period, anatomical characters (number of veins in the coleoptile), and size of stomata, the group of 28-chromosome wheats, as shown by our comparative investigations, surpasses the 42-chromosome group. At the same time there have been discovered not only morphological but also fundamental ecological-physiological differences which permit us to use the 28-chromosome group in obtaining new and necessary combinations of characters. Certain species, for example, *T. dicoccum*, are differentiated over their wide areas by series of sharply distinct ecological-geographical groups, which differ in dozens of characters, including the agriculturally important characters of immunity from rust, smuts, powdery mildew, and other diseases. In their basic areas, the 28-chromosome group of species reach the limit of their culture in the mountainous regions of Abyssinia. Among them there are both extremely xerophytic types (for example the Syrian hard wheat) and extremely hygrophytic types (typical English wheats—*T. turgidum mediterraneum*).

Among the group of cultivated 28-chromosome wheats are found the unusual *T. timopheevi* and wild forms of *T. dicoccoides*. Although they belong to the same category of species as the hard wheats according to chromosome number, they have genetic peculiarities which is observed in their partial sterility in hybridization with other species of the same chromosome number. *Triticum timopheevi* is particularly distinct in this regard. As has been shown by KIHARA, some of its chromosomes are not homologous with those of other wheat species. *The breeding potentialities of the group of 28-chromosome wheats, as has been shown by recent investigations, are much greater than had been previously conceived.* The ecological adaptation of this group is no less than that of the 42-chromosome group. This fact, previously unknown, must be used to a maximal extent in present-day breeding.

Parallelism of Hereditary Variations in Wheat Species:— The systematic study of wheat species and the specific properties of the species shows a striking parallelism in the characters of species which are genetically and geographically distinct. The investigations of recent years have disclosed a great number of new facts. In the foregoing table is given in concise form a series of variations of those species which have been studied in most detail, and for which we have sufficient material. There are included only qualitative characters, as we commonly use this term. We have omitted quantitative characters, since in every species these vary from minimal to maximal. For this reason the qualitative characters appear to be more indicative of parallelism.

According to head characters, glume form, grain color, presence or absence of ligules, and vegetative characters, all of the species show a striking fundamental parallelism. Many characters which not long ago were considered to be systematically specific for soft wheat, such as the presence of awnless forms,

Parallelism of Hereditary Variations in Wheat Species[1]:—

CHARACTER	SUBDIVISION OF CHARACTER	*Tr. vulgare* 2 n = 42	*Tr. compactum* 2 n = 42	*Tr. durum*[2] 2 n = 28	*Tr. turgidum*[3] 2 n = 28	*Tr. persicum* 2 n = 28	*Tr. dicoccum* 2 n = 28	*Tr. dicoccoides* 2 n = 28	*Tr. monococcum*[4] 2 n = 14
Awnedness	A. Awned	+	+	+	+	+	+	+	+
	B. Short-awned	+	+	+	+	+	+	+	+
	C. *inflatum*	+	+	..	+	..	+	..	..
	D. Awnless	+	+	+	+	..	+	..	..
Compactness of the head	A. Loose	+	+	+	+	+	+	+	+
	B. Compact	+	+	+	+	+	+	+	+
Form of the head	A. Club-shaped	+	+	+	..	+	+	..	+
	B. Ordinary	+	+	+	+	+	+	+	+
Color of the mature head	A. White or straw-yellow	+	+	+	+	+	+	+	+
	B. Red	+	+	+	+	+	+	+	+
	C. Black with white background.	+	+	+	+	+	+	+	+
	D. Black with red background..	+	+	+	+	+	+	+	+
	E. Gray	+	+	+	+	+	..	..	..
Hairiness of glumes	A. Smooth	+	+	+	+	+	+	+	+
	B. Hairy	+	+	+	+	+	+	+	+
Waxy layer on the head	A. Present	+	+	+	+	+	+	..	..
	B. Absent	+	+	+	..	..	..	+	+
Color of edges of glumes	A. Black edges	+	+	+	+	+	+	..	..
	B. Without black edges	+	+	+	+	+	+	+	+
Character of glume	A. Fine (*tenerum*)	+	+	+	+	+	+	+	..
	B. Coarse (*rigidum*)	+	+	+	+	..	+	+	+
Form of keel teeth	A. Sharp	+	+	+	+	+	+	+	+
	B. Blunt	+	+	+	+	..	+	+	+
Color of keel teeth	A. Black	+	+	+	+	..	+	..	..
	B. Color of the glume	+	+	+	+	+	+	+	+
Character of awns	A. Coarse	+	+	+	+	..	+	+	+
	B. Fine	+	+	+	+	+	+	+	+
Color of awns	A. White	+	+	+	+	+	+	+	+
	B. Red	+	+	+	+	+	+	+	+
	C. Black	+	+	+	+	+	+	+	+
	D. Only teeth colored black	+	..	+	+	..	..	..	..
Smoothness of awns	A. Toothed	+	+	+	+	..	+	+	+
	B. Smooth	..	..	+	+	..	..	..	..
Aristiform teeth	A. Present	+	+	+	+	+	..	..	..
	B. Absent	+	+	+	+	..	+	+	+
Branching of the rachis	A. Simple	+	+	+	+	+	+	+	+
	B. Branched	+	..	..	+	..	+	..	..
Hairiness of the rachis	A. Strong	+	+	+	+	+	+	+	+
	B. Weak	+	+	+	+	+	+	+	..
Color of the pollen	A. Yellow	+	+	+	+	+	+	+	+
	B. Violet	+	+	+	+	..	+	+	..
Color of the grain	A. White	+	+	+	+	+	+	..	+
	B. Red	+	+	+	+	+	+	+	+
	C. Violet	..	..	+	+	..	..	..	..
	D. Green	+	..	..	..	..	..	..	+
Form of the grain	A. Rounded	+	+	+	+	+	+	..	..
	B. Angular	+	+	+	+	+	+	+	+
Consistency of the grain	A. Vitreous	+	+	+	+	+	+	+	+
	B. Mealy	+	+	..	+	..	+	..	..
	C. Waxy	..	..	+	+	..	..	..	..
Presence of ligule	A. With ligule (*ligulatum*)	+	+	+	+	+	+	+	+
	B. Without ligule (*eligulatum*)..	+	+	+	..	..	..	..	..
Hairiness of seedling	A. Smooth	+	+	+	+	+	+	+	+
	B. Short-haired	+	+	+	+	..	+	+	+
	C. Velvety	+	..	+	+	+	+	+	+
	D. Ciliate	+	..	+	..	..	..	+	+
Hairiness of the leaf sheath	A. Smooth	+	+	+	+	+	..	+	+
	B. Short-haired	+	+	+	+	+	..	+	+
	C. Velvety	+	+	+	+	+	+	+	+
	D. Ciliate	+	+	+	..	..	..	+	+

PARALLELISM OF HEREDITARY VARIATIONS IN WHEAT SPECIES (*concluded*) :—

CHARACTER	SUBDIVISION OF CHARACTER	*Tr. vulgare* 2 n = 42	*Tr. compactum* 2 n = 42	*Tr. durum*[2] 2 n = 28	*Tr. turgidum*[3] 2 n = 28	*Tr. persicum* 2 n = 28	*Tr. dicoccum* 2 n = 28	*Tr. dicoccoides* 2 n = 28	*Tr. monococcum*[4] 2 n = 14
Hairiness of the edge of the leaf sheath	A. Without hairs	+	+	+	+	+	+	+	+
	B. Hairy	+	+	+	+	+	..	+	+
Color of the stem at maturity	A. Green	+	+	+	+	+	+	+	+
	B. Violet	+	+	+	+	+	+	+	..
Color of the stem after maturity	A. Yellow	+	+	+	+	+	+	+	+
	B. Violet	+	..	+	+	..	..	+	..
Habit of life (under uniform conditions)	A. Spring-type	+	+	+	+	+	+	+	+
	B. Winter-type	+	+	+	+	..	+	+	+

[1] The table is mainly limited to "qualitative" characters; similar parallelism is shown by all quantitative characters.
[2] Including subsp. *expansum* Vav. and subsp. *abyssinicum* Vav.
[3] Including subsp. *abyssinicum* Vav. and subsp. *mediterraneum* Flaksb.
[4] Including *T. aegilopoides* Balan.

forms with inflated awns, etc., were found in our expedition of 1927 in north Abyssinia among hard wheats, and probably will be found in the "Persian wheats." Eligulate forms which were first found in soft wheats in Palmyra, were later discovered in hard and club wheats.

This circumstance permits us to suggest a general system of classification based on parallelism which will simplify the study of diversity. At the same time it is necessary to have in mind that a morphological and physiological similarity in characters may result from different genetic backgrounds, which is clearly borne out by the different numbers of chromosomes in the different species.

The Genera Aegilops, Secale, Haynaldia, and Agropyrum:— To complete our survey of the genetic potentialities of wheat, it is necessary to have in mind that in recent years there have been subjected to very detailed investigation not only cultivated and wild wheats, but also the wild genera with which they will hybridize; first of all, different species of the genus *Aegilops*. We have today the two good monographs of Professor ZHUKOVSKI (1929) and EIG (1930), supplemented by the excellent cytological investigations of all species of *Aegilops* carried out by SENYANINOVA-KORCHAGINA. Likewise there are detailed investigations of other neighboring genera such as rye, *Haynaldia,* and others. Also the species of *Agropyrum* have been subjected to investigation, although not as yet sufficiently. There have been discovered a number of new species of *Aegilops* and *Secale* and intraspecific potentialities have been studied. There has been found to be a marked parallelism in heritable variations between species of wheat and those of other closely related genera. No other group of plants has been subjected to such careful differential systematic-geographical and cytological investigations as the wheats and the genera closely related to them. For studying the evolutionary process on a broad scale this group has unique possibilities.

Choice of Initial Materials in Wheat Breeding:— In approaching the question of wheat breeding, the breeder must consider the great potentialities of the 28- and 42- chromosome wheats, among which there are valuable genes that are indispensable for creating ideal types of wheat. In our present understanding, a character is not equivalent to a gene or a group of genes. Char-

acters, in practical understanding, are always associated with definite conditions for their expression; a character is a total result of development; however, to a considerable extent we can direct the distribution of characters in nature, and knowing the geography of valuable characters, we can assemble them for breeding purposes.

Thus in the group of hard wheats, systematic-geographic and physiological investigations have revealed particularly valuable wheats in Syria and Palestine characterized by round grain of high quality, early maturity, comparatively low habit, suitability for harvesting by combine, sturdiness, straw that does not lodge, with smooth awns, a rapid tempo of development during the first period of growth, heat resistance during the period of ripening, and resistance to soil dryness. This type of wheat when tested, showed itself to be suitable to both irrigated and dry land culture in Azerbaidzhan, and today is widely cultivated in this region.

On the island of Cyprus have been found early forms with short straw and productive heads. This group evidently has resistance to attack by larvae of the Swedish fly. The hard wheats of Asia Minor are characterized by large grain, early maturity under the conditions of North Caucasus and Ukraine, and resistance to fusariose. Egypt has early hard wheats that are low-growing with stiff straw. The hard wheats of Spain, and also those of northern French Africa are noteworthy for their high productivity, good tillering, leafiness, large grain, late ripening, and resistance to rust. The hard wheats of the mountains of Arabia (Yemen) are characterized by their extreme earliness and low growth under different conditions in SSSR.

Iran and Trans-Caucasus, according to the specimens of wheat tested under the conditions of North Caucasus and Ukraine, include hard winter wheats with tall straw, good productivity, and large grains.

Abyssina contains original awnless, early-ripening hard wheats which react to a shortened day. *T. persicum* and *T. timopheevi* have, as has already been seen, an exceptional immunity from diseases.

All of the English wheats, which are concentrated principally in southern Europe (Mediterranean subspecies), are characterized by exceptional yields and late ripening under ordinary conditions of culture. These wheats contain the genes for productivity.

Among the *soft* wheats, much interest attaches to the genic potentialities of Afghanistan. The Afghanistan wheats are outstanding in their resistance to shattering, their heat resistance, and their earliness under the conditions of central Asia. The high-mountain winter forms of Afghanistan are noteworthy for their cold resistance. The Indian soft wheats are distinguished for their early maturity, vitreous grain, low, stiff straw, and non-shattering; under our ordinary conditions they are drought-resistant.

The Chinese and Japanese soft wheats are noteworthy for their early maturity and low straw.

The soft wheats of Asia Minor, which are predominantly of spring type, are distinguished by being awnless, non-shattering (with light threshing), and are comparatively early. The Scandinavian soft wheats are distinguished by their high productivity, good head type, stiff straw, resistance to shattering, cold-resistance, preference for moist conditions, and immunity against disease.

The Australian, as well as the South African breeding wheats are distinguished by their early maturity, drought-resistance, stiff straw, productive heads, and resistance to disease.

The Argentine breeding varieties are noteworthy for their resistance to

stripe rust, productivity, large grain, early maturity, and suitability for harvesting with the combine.

Many breeding varieties of wheat of the United States and Canada are exceptional in their early maturity, immunity from diseases and fine-appearing grain.

The question of initial materials is determined to great extent by the region or locality where the breeding work is being developed. For example, in Central Asia or in Trans-Caucasus the local assortments of wheat are rich and varied in their populations, so that naturally the first problem must be to study the local materials, isolating the most valuable forms and reproducing them.

There is no doubt that also within the limits of the European part of the Union, local materials must be the basis for breeding work, as has actually occurred in the early stages of wheat breeding. *For final improvement of wheat, great and decisive significance rests in the planned use of the world diversity of wheat.* As has been shown in actual practice, improvements in wheat culture in a number of new regions, such as U. S. A. and Canada, have been based principally on the use of wheat from our region. A number of the breeding standards of winter wheat in the United States at the present time are our ordinary local Ukrainian and Crimean varieties. The winter wheat varieties brought by the Russian Mennonites in emigrating to U. S. A. are the basis of present-day wheat culture in North America. From the world collection of wheats gathered by the Institute of Plant Industry, there have been isolated a number of Siberian, Palestine, and North African forms which are superior in yield and in other valuable qualities (round grain; stiff, low straw; suitability for mechanical harvesting) which are better than the local varieties under the conditions of Azerbaidzhan and southeast Ukraine.

Although wheat, in general, appears to be a plant with varieties which are comparatively specialized, nevertheless in many ecological types there is observed a high degree of ecological plasticity. For example, the Saratov wheat "Lutescens 062" is suited to Amur Province as well as to the very different conditions of the Lower Volga region and Priamur. The spring wheat "Caesium 0111" is fully suitable for a wide area between 51° and 57° North Lat., from Poland to the Pacific Ocean. The Carpathian winter wheat, Banatka, from which have been derived "Moskovskaya 2411," "Ivanovskaya," and "Durable" is widely adapted to the non-chernozem soil regions. This circumstance permits the transfer of varieties from one region to another. A number of Canadian varieties such as "Garnet" and "Preston" appear to have value for our northern regions.

The Australian variety of spring wheat, "Aurora," which was produced by the breeder Farrer, is as desirable, according to the data from tests in Leningrad Province, as "Novinka," the best of our improved varieties. Some of the best varieties produced by the breeder Klein and brought by us from Argentina, where they are widely grown, have shown in a series of tests in the Leningrad region during two years (1933-34) that they are significantly superior to "Novinka" both in amount of yield and in quality of the grain. In addition they are characterized by resistance to diseases and to shattering. The data of two years' testing have shown the possibility of deriving from Argentine varieties of spring wheat, forms which are at least equal in some areas to the recommended basic variety of Leningrad Province, "Novinka." These facts show how far afield we must go to bring together initial materials even for practical variety testing. The basic collections in the nurseries of breeding stations must include as great a diversity of botanical and ecological types as

possible, from the breeders throughout the world, as well as our own native standard varieties.

Ecological Classification of Wheat:— For purposes of breeding the question of the ecological classification of varieties is particularly important. The Italian student Azzi first introduced very clearly the idea of an ecological classification of wheat. His works on wheat ecology, particularly his noteworthy work on the ecology of Italian wheats, can be regarded as a model of this type of study. In the investigations of Azzi there have been successfully combined three factors: a knowledge of the breeding problem, a world assortment of wheats, and a consideration of agrometeorology. He introduces, in the geographic characterization of varieties, such breeding objectives as quality and resistance to disease, heat, cold, drought, excessive precipitation, and other unfavorable factors. In his extensive monograph, "Le Climat du Blé dans le Monde," Azzi has courageously attempted to work out an ecological classification of the wheats of the entire world. Despite major deficiencies in this work, it unquestionably deserves attention from a methodological viewpoint. Azzi's work found its followers. An interesting study was published not long ago by Papadakis on the wheats of Greece, in which critical attention is paid to the fundamental works of Azzi.

Great importance in the ecology of different varieties attaches to *temperature relations,* both in the sense of reaction to vernalization and in that of resistance to low and high temperatures in different growth stages. The Central Asiatic wheats, for example, ripen only at high temperatures, while the northern Russian varieties can ripen at low temperatures.

Wheat varieties are quite distinct in their reaction to *day length*. In many northern forms of wheat of western Europe and Russia, the short days of the south retard the heading phase. The northern long day accelerates the onset of this phase. Many Central Asiatic and Iranian varieties show little response to changes in length of day.

Marked varietal differences in wheat are shown in relation to *moisture*. Northern forms are favored by high moisture throughout the entire vegetative period. The Central Asiatic varieties are favored by moisture in the first period of growth while they are comparatively quite drought-resistant after the boot stage (E. F. Palmova).

Varieties differ sharply in their *rhythm of spring development*. Many western European forms under our conditions develop slowly during the spring. The northern varieties of Siberia and the European part of SSSR develop much more rapidly, while the Central Asiatic varieties are distinguished by their exceptionally rapid growth.

The ecological characters include *varietal differences in developmental stages,* determining the form of life under given conditions: spring or winter cycle, early or late maturity. Included in the ecological characters is also the potency of the plant in the sense of producing leaves, stems, and heads, and productivity itself. We distinguish types of "intensive" and "extensive" culture.

Azzi attached great significance to the ecological character of resistance to diseases, as associated with environmental conditions.

Even such a character as color of the heads is evidently not without ecological significance, since in the extreme north occur almost exclusively spring red-headed forms, while in the south are concentrated more of the white-headed wheats.

The species of wheat are rather sharply delimited ecologically in relation

to their specific areas of development. Hard wheats (subsp. *expansum*) are peculiar to warm steppe climates with a moist spring. The hard wheats, while they are rather resistant to heat during the ripening period, undergo low temperatures earlier in their development, and ordinarily in the Mediterranean region they are sown in the fall. *T. turgidum* subsp. *mediterraneum* requires much moisture and its basic area is in the coastal moist climate. Short day-length hastens heading of *T. turgidum* more than of *T. durum.*

T. vulgare as a species is strikingly universal and appears to be cosmopolitan. *T. persicum* is resistant to low temperatures both in early growth stages and in the period of ripening.

German investigators today classify all German varieties into five types. Thus BREKKER in his recent "Encyclopedia of Agriculture" in the volume "Pflanzenbau," divides all wheats into five types. To the first belong the *hygrophytes,* varieties which are grown in conditions of high moisture, requiring warmth and being very sensitive to fertilization. To this group belong the typical squareheads, for example "Holland Wilhelmina," the Svalöf "Extra Squarehead," and the group of Dickkopfweizen, which have been derived from the English squareheads.

In the second group belong the *hygromesophytes* which are characterized by high productivity. This second group is closely related to the first.

The third group, which is most widely grown in Germany, includes the *mesophytes.* It is noteworthy for its relatively high productivity. The group is distinct from the last in its comparative weather resistance, even in unfavorable years. The third group is subdivided into three subgroups, the *first* growing on rich clay soil, the *second* on lighter soil, and the *third* on soils that are almost sandy. The majority of the typical German wheats belong to this third group, including such varieties as Rimpau, Frühere Bastard, Kriwener 104, Cimbal, and Silvester.

A fourth group includes the *mesoxerophytes.* These are wheats with the least requirements of all, growing on soils similar to those adapted to rye.

And finally, there is a fifth type—*xerophilic wheats,* which are adapted to dry climates. To this belong various varieties of Banatka wheats, hard wheats, spelts, emmers, and einkorns. In Germany the majority of the wheats are winter type, to which this classification refers.

In a similar fashion the spring wheats may be divided.

Investigations of the great world wheat assortment at the Institute of Plant Industry permit us to outline schematically a basic ecological grouping of wheats. E. F. PALMOVA has described the following four basic ecotypes for *soft* wheats of the Old World:

1. Moist climate type.
2. Steppe type.
3. Type of desert and semi-desert zone.
4. Type of moist, high mountainous areas.

In the first type, wheats of moist climates,[65] we distinguished the following ecological-geographical groups of varieties.

a) *West-European group of winter wheats* which are distinguished by their vigorous development, leafiness, high tillering capacity, and large heads; the grains are large and mealy; productivity is high; the requirement for warmth is lower than in the other types, but there is a particularly high requirement for day length. All of the varieties have a high requirement for air and soil mois-

[65] This ecological classification is basically that of E. F. PALMOVA. In it we have made a few corrections in the geographical terminology, and also a number of changes based on our own observations. See E. F. PALMOVA. [Introduction to wheat ecology.] 1935.

ture, fertilization, and tillage. Here belong Swedish, Dutch, Danish, English, and Belgian varieties.

b) *Mediterranean group of winter wheats, distinguished from the preceding group by their lower degree of winter resistance and greater requirement for warmth.* Among them are found also semi-winter types. To this group belong many varieties of France, Algeria, Italy, and the Balkan Peninsula.

c) *Central European group* consisting of winter wheats with less requirement for all life conditions than wheats of the preceding two groups, corresponding to their comparative *extensive* culture. Comparatively winter- and drought-resistant. To this group belong many Polish, local German, Lithuanian, Estonian, and Northwest Russian winter wheats (for example "Kostromka") and wheats of N. W. Ukraine (for example "Visokolitovskaya").

d) *Wheats of western Asia* (Japan, Eastern China, Korea), principally of winter or semi-winter types, very early in ripening, requiring warmth, low growing, with yellow-green leaves, and small grains. This is a highly productive group which is very valuable for hybridization with European varieties. It has been used by STRAMPELLI for creating the well-known Italian variety, Ardito.

e) *Spring wheats of moist climates.* To this group belong such varieties as "Kolben," "Aurora," and "Blue Dame" in Sweden and Germany and "Tamm" and "Ruskea" in Finland. These have a comparatively high heat requirement and are average and later maturing varieties.

f) *Northern early-maturing spring varieties.* To this group belong the northern Russian varieties, both of the European part of Russia, and of eastern Siberia. This group has the least warmth requirement of all, and is characterized by small grain, comparatively few leaves, and thin straw. Here we find, for example, *T. vulgare* v. *ferrugineum sibericum* Flaksb., and also the variety *erythrospermum irkutianum* Pissar.

A general property in wheats of the moist climate type is a high requirement for moisture and for a prolonged length of day.

The *steppe type* includes both winter and spring wheats. In SSSR this type appears to predominate. Its winter varieties occupy the steppe regions of the European part of Russia while the spring varieties are found mainly in the East and Northeast. This type has well-marked xerophytic features, thin straw, average tillering, and, compared with the preceding type, few leaves. The winter wheats of this type are early ripening and resume activity in the spring very early. Where there is a scanty snow cover they are more winter-resistant than wheats of moist climates. Typical representatives of this group are "Krimka" and "Banatka." Of the improved Soviet varieties, this group includes "Ukrainka," "Cooperatorka," "Stepnyachka," "Sedouska," "Krimka," "Kanred" (U. S. A.), "Minhardi" (U. S. A.), and "Minturki" (U. S. A.).

The spring varieties of the steppe type include "Poltavka," "062" of the Saratov Station, "Hostianum" of the Saratov Station, "Novokrimka," "Rusak," "Leda," "Preston," "Garnet," "Marquis," and "Florence" (South Africa), as well as a number of wheats of Asia Minor. The spring wheat "Stepnyachka" occupies a wide area and shows great plasticity. In SSSR this type occupies a dominant position in western Siberia, in the steppes of Trans-Volga and Ural, and extending up to the foothills of Trans-Caucasus. Winter forms are found in Crimea, Ukraine, North Caucasus, and Kirgizstan. In western Europe "Stepnyachka" is principally distributed in central Spain, Portugal, Rumania, Hungary, Czechoslovakia, and Yugoslavia; wheats of this type are widely grown in the United States with spring forms in the northern U. S.,

particularly in North and South Dakota and in Canada, and winter forms in Kansas and Nebraska. Steppe wheats are quite resistant to spring drought. On the whole, both winter and spring steppe forms are favored by light, with heading delayed when they are grown in the South.

Desert and semi-desert types of wheat are cultivated either with or without irrigation, and are widely distributed in Central Asia, India, Afghanistan, Western China, and in North Africa. This type is distinguished by its medium to low growth, comparatively stiff straw, coarse leathery leaves, presence of a waxy layer on stems and leaves, *coarse heads, non-shattering grain, difficult milling, coarse awns, and frequent brittleness* (*rigidum* type) ; it includes both winter and spring varieties.

All the wheats of this type are distinguished by their early maturity and rapid tempo of development in the first period of life. Although they have a considerable water requirement in the first half of life, wheats of this type, thanks to their earliness, produce yields in the Trans-Volga region even in dry years.

Among this type there are some Indian forms which are distinguished by their less coarse heads. The wheats of India are entirely early maturing. Many of them are noteworthy for their fine-appearing grain. Because of their comparative plasticity, their heat-resistance, and their early ripening, the wheats of India deserve particular attention. The majority of the Indian wheats appear to be of spring type.

Wheats of moist high mountainous regions are particularly well represented in the high mountains of Central Asia, Palmyra, in the high mountains of Afghanistan, and in Kashgar and Mongolia. Wheats of this type are distinguished by their leafiness and high water requirement. Under the conditions of the European part of SSSR, they are very susceptible to fungus diseases, and suffer from drouth if water is deficient.

The peculiar ecological conditions of the high mountainous regions of Central Asia have resulted in the production of original types of wheat which are little suited for cultivation in northern regions where they ordinarily suffer severely from fungus diseases.

Besides the enumerated four types there may be distinguished supplementary intermediate types occupying positions between the first type, of the moist climates, and the second, steppe type. In Australia, Argentina, and South Africa in recent decades there has been described a peculiar type which does not fit into the scheme given. Soft spring wheats of Australia and South Africa, obtained by hybridizing extreme ecological types, are distinguished by early ripening, stiff straw, large grains, and a requirement for water in the early period, together with comparative drought-resistance in the second period of growth. The Argentine wheats are noteworthy for their non-shattering, adaptation to combine harvesting, wide distribution in this region, high water requirement, and characteristic large grain. Under our conditions they behave as spring types, and some of them evidently may be used by us in the north.

The ecological classification given above applies to soft wheats.

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Hard wheats occupy an area which is much more limited, being principally cultivated by us in western Siberia and North Caucasus. They are also grown on the shores of the Mediterranean Sea and in comparatively small amounts in northern regions of U. S. A. and in the southern prairies of Canada. The primary areas of distribution of the hard wheats appear to be steppe zones.

The hard wheats are suited for culture on chestnut soils in hot and comparatively dry regions. On the basis of the complex of morphological, ecological, and geographical characters, in our "Wheats of Abyssinia" (1931), we have divided hard wheats (*T. durum* Desf. *in sensu lato*) into two subspecies:

1. *T. durum abyssinicum* Vav. The basic area is the mountains of Abyssinia and Eritrea. This is a mountain type of hard wheat. It is characterized by a large number of vascular bundles in the coleoptile (4-6) and the presence of a considerable number of endemic forms, such as violet-grained races with long awn-like processes on the glumes, awnless and semi-awned forms, and forms with seedlings which are pigmented with anthocyanin (violet). This subspecies on the whole is characterized by its low growth, small heads, leafiness, early maturity, preference for considerable water, relative susceptibility to leaf rust, and small warmth requirement. Its leaves differ from those of other hard wheats in having a waxy covering; in external appearance the heads remind one of those of soft wheats. Abyssinian hard wheats are exclusively of spring type. Their productivity is not great. The greatest degree of earliness is found in the hard wheats of Arabia which are referred to *T. durum abyssinicum.* In this respect they occupy first place among all known wheats. Within this subspecies there appears a great polymorphism in head and grain characters.

2. *T. durum expansum* Vav. The basic areas are the Mediterranean region, the southeast European part of SSSR, and western Siberia. This is distinct from the Abyssinian hard wheats in its large heads, long awns, large grain, thick, tall straw, strong development, comparatively late ripening, requirement for warmth, smooth leaves, and, on the whole, resistance to leaf and stripe rust, powdery mildew, and to some extent, stem rust.

This subspecies is divided into the following sections:

a) *africana* Vav. with *compact heads,* long awns, and resistance to rust. Basic area: Morocco, Algeria, and Tunisia;

b) *mediterranea* Vav. includes forms of *intermediate compactness of heads;* comparatively late maturing, large seeded forms which mill with difficulty. Geographically this section is adapted to French North Africa, Tripolitania, southern Italy, southern Spain, Syria, Palestine, the southern part of the Balkans, and to some extent, Egypt. It is widely distributed throughout the Mediterranean region. For normal yields this type of hard wheat requires ample moisture in the first period of growth. The wheats of this type in the Mediteranean region are commonly sown in the fall;

c) *europea* Vav., most widely distributed at the present time in Europe, Asia Minor, Western Siberia, U. S. A., and Canada. To this section belong our "Garnovka," "Beloturka," and "Kubanka." In comparison with the preceding section, forms of *T. durum expansum europea have comparatively loose heads* and are earlier. They are distinct from *mediterranea* forms in lower growth, less leafiness, smaller heads and grains, and less requirement for warmth. The forms are exclusively spring type.

In addition, in the subspecies *T. durum expansum* we distinguish three geographical groups of forms:

a) *Syrian-Palestine* group with compact heads (about four spikelets per 1 cm.) with short awns, *round,* vitreous *grain,* and low growth. This group, from the standpoint of breeding, deserves particular attention because of its suitability for combining, non-lodging, yield (under conditions of Azerbaidzhan), and fine appearing grain. It occurs, in addition to Syria and Palestine, in Trans-Jordan, Egypt, and Asia Minor. Ecologically, in its basic area, it is adapted to semi-desert conditions. It is cultivated in great quantities in Trans-Jordan and Syria on non-irrigated land. It is distinguished by its low growth, early maturity, narrow leaves, high degree of drought resistance, and rapid tempo of development. It is commonly sown in Syria in late fall or winter when the rains come. It needs a considerable supply of water during its early period of life. This may be considered a branch of the section *africana* Vav.;

b) *Hard wheats of Egypt* are distinguished by their early maturity, low growth, and susceptibility to stripe and leaf rust. They differ from the preceding forms in their *coarse*

heads, coarse hard awns, and also their coarse and short hairy leaves. They may connect *T. durum abyssinicum* to *T. durum expansum;*

c) *Eligulate hard wheats of Cyprus* and related ligulate hard wheats of the Mediterranean Islands. They are distinguished by small heads. Systematically they are adjacent to *T. durum europeum* Vav.

3. *Hard wheats of Trans-Caucasus* are characterized by winter or semi-winter form of life when sown in North Caucasus or Ukraine. They respond well to vernalization which markedly accelerates their development. This type is distinguished by its tall growth, leafiness, large heads, and high productivity, reminding one, in this respect, of *T. turgidum.* To the same group belong certain forms of wheat of central and eastern parts of Asia Minor and North Africa.

T. turgidum, in its subspecies *mediterraneum,* ecologically is adapted to the coastal regions lying along the Mediterranean Sea. This subspecies is characterized by strong development, leafiness, and high requirements for fertilization and tillage. The forms are either winter or semi-winter type; they are moisture-loving. The vegetative period is long, whether they are planted in the fall or spring. Here belong the latest of all forms of wheat. Their winter resistance is low.

In the blossoming stage all forms of this subspecies evidently react favorably to a shortened day-length.

From the Mediterranean subspecies is sharply distinguished the Abyssinian subspecies (*T. turgidum* subsp. *abyssinicum*) which contains exclusively spring, early-maturing forms. Ecologically they are not distinct from *T. durum abyssinicum.*

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T. dicoccum repeats the ecological classification of the soft wheats in being divided into four types: the first is the *type of moist climates* in which we find the late ripening emmers of Germany and Spain. The second is the *steppe type* where belong the emmers of RSFSR and ZSFSR. The third type of the *semi-desert* is peculiar to Arabia and India, and the fourth—*high mountain type* which is peculiar to Abyssinia, is distinguished by its water requirements, and ecological features resembling those of *T. durum abyssinicum.*

Club wheats—*T. compactum*—according to their ecological differentation, are reminiscent of *T. vulgare.* They are divided into:

a) *West European water-loving type;*

b) *Mountain-Caucasus* type with small warmth-requirement during the period of ripening, resistance to low temperatures in the spring, and small requirement for soil and agronomic culture;

c) A type *adapted to mountainous deserts* (Palmyra, Mongolia); and

d) *Afghan dwarf wheat,* distinguished by its unique head and large grains which can be threshed out only with difficulty; it is adapted to high mountainous regions.

T. spelta is distinguished by its high requirements for soil and tillage and its need for water; it includes both winter and spring forms.

T. sphaerococcum is noteworthy for its heat resistance, low growth, and leathery leaves.

T. vulgare compositum Tum. (*T. vavilovianum* Jackubz.) has the feature of extreme xerophily. It is characterized by having few, leathery leaves with a marked waxy layer. The forms are of winter type and late in maturing. The grain is mealy.

T. macha consists of winter forms with a large leaf mass and high water requirements.

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T. persicum consists of spring forms. Ecologically they are characterized by their ability to grow at low temperatures. Among the 28-chromosome group of wheats they have the least heat requirement of all, and are high-mountain wheats of the temperate zone. They can tolerate high moisture during the ripening period, but have little heat-resistance. They are immune from stem, leaf, and stripe rust, and from powdery mildew. Their small heat requirement and their immunity gives this group of varieties particular value for breeding for northern regions.

T. timopheevi is extremely indifferent to all the conditions of growth and it is particularly resistant to attack by fungus diseases. The forms are of spring type and comparatively late in ripening.

T. monococcum, on the whole, is characterized as a steppe type, tolerating extreme differences in growing conditions. All the forms are comparatively late in ripening. A valuable property of this species is its immunity from fungus diseases.

The wild wheats *T. dicoccoides* and *T. aegilopoides* are distinguished by their broad tolerance of conditions of growth and their xerophily. They are mainly winter types. Among the forms of *T. dicoccoides* are sometimes encountered spring races.

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A comprehensive basic botanical classification of wheat into ecological groups is particularly necessary for breeding, since the breeder must select forms for definite combinations of temperature, light, and moisture factors. In the future, physiological investigations must give us a more exact method for defining the wheat types, in particular for studying varietal differences according to the stage of plant development. The future systematist must be basically a physiologist.

Vernalization of Wheat:— The ecological grouping leads us to the questions associated with the study of stages of development and vernalization which have been worked upon by T. D. Lisenko. Vernalization discloses new horizons in the use of the world assortment of wheats. Experiments carried out in 1932, 1933, and 1934 in different regions of SSSR—from Odessa and Kuban to the Arctic Circle and Khibin—have shown reliably the positive response of wheats to vernalization. The experiments have involved the entire world collection of wheats. The different varieties differ in their requirements for moisture in the seed at the time of vernalization, temperature, and time of vernalization. Almost all the winter forms could be easily vernalized at low temperatures from 0° to 5° C. during 35-60 days, and were converted into spring types. The semi-winter forms were vernalized between 5° and 10° C. for 25-30 days and these became comparatively early spring types under ordinary conditions in the European part of SSSR. For hastening the growth of spring forms it was necessary to vernalize for fewer days, but at higher temperatures. In general, for soft spring early-ripening forms, vernalization was carried out for 5-10 days at temperatures from +10° to +12° C., and for hard wheats (Garnovka type) for 10-14 days at +2° to +5° C. To each 100 kg. of grain, depending on the variety, there was added from 31 (for early spring types) to 37 kg. (for winter types) of water.

The spring Mediterranean forms and the Trans-Caucasus late ripening hard wheats reacted very strongly to vernalization, and the Abyssinian forms somewhat less so. Winter wheats of southern regions which were unable to grow under the ordinary conditions of central and northern Russia, when vernalized, developed to maturity. Even the latest ripening wheats, for example the Eng-

lish *T. turgidum* which is distinguished by high productivity, after vernalization ripened under the conditions of the Southeast and to some extent in Leningrad (Detski Village), *i.e.*, in areas where they normally could not grow, because of their late maturity if sown in the spring and low degree of winter resistance if sown in the fall. The application of vernalization to wheat has particular interest for the breeder, since it makes it possible for him to include southern forms with little winter resistance in developing forms for northern conditions.

Until recent times, breeding as well as genetics had been worked upon primarily in Western Europe and North America, with their limited temperature conditions, where it would not be possible to make good use of initial materials of southern wheats. Actually, until recently the European geneticist and breeder has worked with only a very small part of the world wheat potentials.

Vernalization is important not only as a means for extending the possibilities of breeding and genetic work, but also for isolating from the world assortment the wholly suitable varieties, combining for our purposes vernalization with the best standard varieties. Vernalization makes it possible for the breeder to include the entire world assortment among his materials. The enormous specific and varietal potentials of wheat discovered in recent years include a large number of valuable genes which have still greater significance in the light of the method of vernalization.

Finally, we must understand that the method of vernalization and the whole subject of developmental stages has great significance in the selection of parental forms for purposes of hybridization.

Environment and Heredity (Non-Heritable Variation, Geographic Variation, and Ecological Plasticity of Wheat Varieties):— Regarding the foregoing ecological grouping of wheat varieties, and the study of growth stages of T. D. LISENKO, we see clearly the great relationship between the phenotype of the wheat variety and its environmental conditions. Along with genotypic variations, no less attention must be given to the effects of environmental factors on individual variation, since these may frequently obscure varietal and hereditary differences causing them to lose their significance. For many characters of wheat it may be very clearly seen how profoundly heritable varietal differences may be influenced by environmental conditions.

Such important characters as vegetative period, winter-resistance, drought-resistance, yield, tillering, immunity from diseases, quality of grain (vitreous, mealy), and chemical composition, are not only determined by varietal differences, but to great extent are related to environmental conditions. By suitable choice of environment, a variety that is winter-resistant under one set of conditions may be made non-resistant under another set. The "hardening" of plants, as has been shown by investigations of present-day physiology, may fundamentally change the cold-resistance and drought-resistance of wheat. Dry air and soil and the presence in the soil of a sufficient quantity of nitrogen may increase the protein content of the grain of a given variety to an extreme limit of 2-3 times. A late-ripening variety may, after vernalization, appear early in ripening. A single variety may have either spring or winter habit depending on the conditions prevailing at the time of sowing. When speaking of the winter or spring habit of wheat varieties, as well as of other properties, such as vitreousness, winter-resistance, drought-resistance, and immunity from diseases, one must constantly have in mind the concrete environmental conditions, particularly those of climate.

The investigations of LISENKO have shown that growing conditions, result-

ing from selection of certain environments, may result in grain that is entirely vitreous instead of the mealy grain produced under normal conditions.

None of these marked changes resulting from the influence of different environmental conditions on plants, is inherited, yet in deciding the question of the yield of given varieties and the quality of the grain, these non-heritable variations have decisive significance.

During the course of its development from sowing to maturity, a wheat variety in its different stages of development is highly dependent on the conditions of the environment. The study of developmental stages brings out very clearly the significance of varietal differences and their response in different stages, both for breeding and for controlling non-heritable variations. As shown by LISENKO, wheat varieties at different stages (temperature, or more properly speaking, vernalization in the blossoming stage) are very distinct in their reaction to external conditions. The complex of external conditions suitable for one stage of development may be entirely unsuitable for the passage of a given variety through another stage of its development.

The entire science of agrotechnique and fertilization essentially has to do with non-heritable or individual variations in the sense both of quantity and of quality of yield. Present-day agronomy is changing more and more from a science of general agrotechnique and fertilization to varietal agrotechnique and to the determination of the relationships between varieties and fertilization. (See Chapter "Variety and Fertilization").

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The extent and diversity of conditions of our region necessarily lead the investigator to a geographic approach in solving breeding problems. The variation of a given plant, a given genotype, in relation to the complex of geographic factors, proceeds according to rule. Length of day and changes of temperature and moisture vary regularly over great geographic areas. In 1926 the Institute of Plant Industry first organized its so-called geographic experiments which involved 115 points from Khibin to the Mervsk Oasis in Turkmenistan and Lithuania (Kovno) to Vladivostok. These points were located in places where there were meteorological stations. In these geographic experiments there were included 40 different species of cultivated plants and 185 different varieties; wheat was particularly well represented, with both winter and spring varieties embracing all the important species. The harvest results (seed, heads, and the entire plant) were subjected to thorough analysis. These experiments, continued for five years and at present being carried out anew with a still greater series of varieties, revealed a shortened vegetative period in most varieties of wheat as they were grown farther northward where there is a longer day during the vegetative period. This rule applied particularly during the first days of vegetation from the seedling stage to heading.

The height of the plants increased in going northward or in ascending to mountainous moist regions. In general, it was determined by the quantity of precipitation in the vegetative period. Tillering appears to be due to a more complicated set of causes.

The content of protein in the wheat grain varied sharply and regularly throughout the extent of the territory of SSSR. On the other hand, the tests showed that some varieties varied in this respect to only a very small extent, for example the Persian wheat (*T. persicum*) which is distinguished by an unusual vitreousness and high percentage of proteins under different growing conditions.

The geographic experiment produced extensive materials for studying the

variation of morphological characters. Although the ordinary morphological racial and varietal characters did not appear to be absolutely constant, but varied with region and time, nevertheless the geographic experiment disclosed a number of characters which were comparatively unaffected by environment. Among these, as the experiment showed, were form and size of the glumes and, in the majority of forms, size and character of the glume teeth. The form and even the size of the grain varied but little. Awned and awnless forms as a rule retained this character under the most varied conditions. Even group immunity from leaf and stripe rust was a character which was very constant over a great area of SSSR under the most varied conditions. The coefficient of variation of such characters as height of plant, tillering, length of leaves, and length of heads was very great, so that these characters are of very little value as criteria for classification.

A single character might be very constant in one race of wheat, and very variable in another. For example, the Kansas wheat Black Chaff was very variable in head color; one year it produced black heads and another year white ones; sometimes on a single plant in one place there were encountered tillers with black and white heads. As a rule the pigmentation of the glumes became deeper to the northward.

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The data of the State variety tests during ten years have brought out facts of primary significance in the breeding and geography of wheat, which are particularly important for devising official agricultural practices with respect to changes in varieties and substitution of varieties during years of crop failure in the different localities.

These data have shown that despite the ordinary narrow specialization of area of all wheat varieties, a number of important winter and spring wheats are strikingly universal. Thus, of the spring wheats the variety "Caesium 0111" produced by the West Siberia Station is wholly cosmopolitan and may occupy a great territory from the Polish border to East Siberia. In 1937 six and one half million hectares were occupied by this variety, *i.e.*, approximately one-fourth of all of the area planted in spring wheat in SSSR.

Equally universal are the Saratov varieties of spring wheat "Erythrospermum 0341," and particularly "Lutescens 062." The latter does well in the whole European part of SSSR and in West Siberia, including the area extending to the Far East and Leningrad Province. In 1937 about five and one-half millions hectares were occupied by this variety.

Of the soft wheats, the same broad universality in North America characterizes "Marquis," which has occupied 70% of all of the spring wheat area in Canada and in addition has been grown on a great territory in the northern United States.

A similar universality is shown by a number of hard wheats, for example "Hordeiforme 0189" produced by the Krasnokutsk Station, "Hordeiforme 010" produced by the Dnepropetrovsk Station, and particularly "Melanopus 069" (Krasnokutsk Station).

In 1937 these three varieties occupied four and one-half million hectares, *i.e.*, the greater part of the area supposed to be planted with hard wheat.

Of the winter wheats there are also a number of very universal varieties such as "Ukrainka," which today occupies more than half of the entire area under winter wheat in SSSR, *i.e.*, no less than five million hectares. The variety "Hostianum 0237" of the Saratov Station, is also characterized by occupying a wide area.

Of the northern varieties, "Moskovskaya 2411" and "Durable" (Erythrospermum 0348) are comparatively cosmopolitan.

It is interesting to note that "Ukrainka," "Durable," and "Moskovskaya 2411" have all been developed from the Pri-Carpathian Banatka.

Of the American winter wheats, the variety "Kanred," which was derived from our Southern varieties is very universal. The Australian variety "Aurora" does well not only in Australia where it was developed, but also in Sweden, Finland, and in northern SSSR. A number of Argentine wheat varieties, which are cultivated there in a subtropical region with an ample water supply and without winter exposure, as we have already shown, give good yields under conditions of the northern region of the European part of SSSR.

Evidently the same universality applies to einkorn and spelt wheats which grow normally under the most diverse conditions.

On the other hand, the majority of present-day foreign varieties of wheat show little plasticity or adaptation to different regions. For example one of the best Canadian varieties, "Kitchener," which has good barrel-shaped grain, is adapted in our region only in a few southern moist regions of East Siberia. The most productive varieties of English wheat (*T. turgidum*) occupy small regions, mainly under the conditions of moist, coastal climates. A large number of wheat varieties produced by Australian breeders have only local significance. The overwhelming majority of winter and spring wheat varieties, as has been shown by the State variety testing experiments, are comparatively narrowly specialized, being adapted only to limited areas. The varieties of wheat in the mountainous regions of Central Asia and Trans-Caucasus, as might be expected, are highly specialized.

In any case, the total ecological plasticity of wheat varieties, including soft and hard wheats and both winter and spring varieties, is very great, which gives a broad scope for breeding work. In this respect, the nature of varietal differences needs further research. Actually we still know very little of the nature of cosmopolitanism versus narrow specialization, not only for varieties, but even for entire crops.

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The attention of the breeder has been primarily directed to the introduction of varieties, to genotypic differences, and to heritable variations. The deeper investigations go, the more we learn of the requirements in wheat breeding, and the more attention we must give to the relationship between environment and variety revealed in individual differences in requirements of agrotechnique, fertilization, and the selection of certain conditions and regions for crop culture. The study of stages of development and of varietal differences in reactions at their different developmental stages, with evaluation of the total result in the sense of quality and quantity of harvest, forces us to give attention to this subject.

The Biology of Wheat Blossoming:— Wheat, as we know, is typically self-pollinating, so that frequently simple, single selection suffices for obtaining necessary and valuable forms. However, practice shows that we are finding less and less uniformity in pure lines and even such an authority on wheat as PERCIVAL considers it is more correct to change the term "pure lines" in wheat terminology to "single lines," since detailed studies of the progeny of single lines ordinarily reveal quantitative and qualitative hereditary differences. The principle of pure lines may be taken only in a relative sense, not in an absolute one. Accordingly it is frequently useful to carry out repeated selection in self-pollinated wheat. JOHANNSEN, particularly in one of his works which is little

known, published in 1906 in the Proceedings of the Third International Congress of Genetics in England, writes as follows: "Pure lines—this is only a genealogical term. . . . It signifies only a guarantee of pure heredity. By mutation or segregation new types or gametes may occur in pure lines just as in genealogical hybrids, although the lines nevertheless remain pure in a genealogical sense; thus, pure lines may be mono-, bi- or polytypic" (p. 103).[66]

In PERCIVAL's opinion, quantitative and qualitative hereditary differences are very common in single lines, and hence it is necessary to resort to repeated selections to obtain new improved forms. This is all the more essential since, according to PERCIVAL's observations in England, in wheat natural hybridization is very rare. The frequency of natural hybridization, according to PERCIVAL's observations during 30 years, did not exceed 10-15 cases per 10,000 plants; mutations in his opinion, were still rarer, about 1-2 cases per 10,000 plants.

Observations of German breeders, beginning with RIMPAU, have also revealed natural hybridization. There are dozens of publications calling attention to natural hybridization in wheat.

Within our region, cross-pollination not infrequently appears in a greater amount. For example in the southeastern European part of the Union, G. K. MEISTER (Saratov) has noted a massive hybridization of wheat with rye in cases when the blossoming of rye coincided with that of wheat. G. M. POPOVA found frequent cases of hybridization of wheat with species of *Aegilops* in Central Asia. We have observed analogous cases of hybridization of hard wheats with species of *Aegilops* in Sicily. M. M. YAKUBTSINER has seen the same thing in Karabach and southern Azerbaidzhan.

The total of published facts shows that evidently the frequency of natural hybridization is greater in regions of dry climates where open blossoming can occur, but even under the conditions of Germany, Belgium, and France, natural hybridization is not rare.

Although we must have in mind the possibility of fertilization by foreign pollen and the appearance of mutations, nevertheless basically we may work with wheat as a typical self-pollinated plant, having recourse where necessary to repeated or even to numerous reselections. Present-day breeding differs basically from that of the time of HALLET based on the study of pure lines (1903), since today actually the majority of breeding stations subject self-pollinated plants to continuous and repeated selection.

We must note the interesting observation of T. D. LISENKO that in some wheat varieties low temperatures retard or inhibit the development of pollen.

The phenomenon of *heterosis* in the first generation of crosses of different wheat varieties belonging to a single species, was determined by ENGLEDOW and PAL (1934) in studying the behavior of hybrids, in comparison with the parental forms, with respect to grain yield and tillering of the plant, and also physiological behavior as seen in germination of the seed of parents and hybrids. Heterosis in wheat, in crosses within the limits of a single species, as is known, does not take the striking form, seen, for example, in corn. It has been shown particularly clearly in crosses of the variety "Little Joss" and "Yeoman." In the first generation some combinations show only weak heterosis, and others fail to show it at all. Nevertheless wheat exhibits heterosis more clearly than barley. In the second and third generations of wheat hybrids, heterosis disappears entirely.[67]

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[66] W. JOHANNSEN: Does hybridization increase fluctuating variability? Report of the Third International Conference on Genetics, 1906, London.

[67] ENGLEDOW, F. L., and PAL, B. P., 1934: Investigations on yield in cereals. VIII. Hybrid vigour in wheat. Jour. of Agr. Science, 24(3): 390-409. London.

It is clear that there are no reliable data demonstrating the so-called "degeneration" of wheat varieties with their ordinary self-pollination. The contamination of wheat with rye and the "transformation" of it into cheat [?], as well as varietal mixtures, are due to other causes, to mechanical mixing or to the effects of natural selection, substituting other forms for the original wheat variety. In particular we must consider the phenomenon of segregation in varieties that are not sufficiently homozygous, and also an inclination of some varieties towards mutation. A number of old wheat varieties such as "Rivet" (*T. turgidum*) and "Blue Cone" (*T. turgidum* v. *iodorum*) have been cultivated in England as definite varieties for several centuries (PERCIVAL, 1934). Many improved wheat varieties such as "Federation," "Wilhelmina," "Marquis," and others have been multiplied for decades without any significant weakening as a result of self-pollination or inbreeding.[68]

Selection and Hybridization:— The majority of wheat varieties cultivated in different regions are the result of simple selection without the use of hybridization. Thus our Soviet wheats, including the improved ones, in the overwhelming majority of cases appear to be the result of simple selection either from local materials or from forms introduced from ancient regions of culture. Our best improved varieties of both spring wheats such as "Caesium 0111," and "062," and winter wheats—"Ukrainka," the Moscow varieties "02411," "02453," and "27," and the Odessa varieties "Cooperatorka," "Stepnyachka," and "Zemka" are forms which have been developed as a result of simple selection from local materials.

All of the wheats primarily cultivated in southwestern Asia, the Mediterranean region, and China have been developed by selection without crossing. The same may be said for India. A number of the best new varieties which are widely cultivated today in India were produced by ALBERT HOWARD by selection from local varieties. The greater part of the winter wheat of the United States, until recent times, has been the result of simple selection from Russian, Ukrainian, or other foreign varieties. The same may be said for Hungary, the Balkans, and Spain.

Almost all varieties of hard wheat cultivated throughout the world are the result of selection. Only in the most recent times have there begun to be introduced into culture hybrid hard and soft wheats, and this is still limited to a rather small quantity.

There is no doubt that for a number of our breeding stations the opportunities of the method of simple selection have not yet been exhausted, and for such regions as Central Asia and Trans-Caucasus it appears to be basic and obligatory.

The earliest experiments on hybridization of wheat were carried out by THOMAS KNIGHT. He first noted natural wheat hybrids in mingled plantings of different varieties. Some of these hybrids, in his words, were superior while others were very poor, but not one of them remained constant.

In 1846 at a meeting of the English Agricultural Society MAUND of Bromsgrove reported obtaining hybrid wheat. The same year HUGH RAYNBIRD ob-

[68] The work of AZZI in Italy appears to be very significant, showing that a single pure line of wheat, after preliminary cultivation in different regions (from Scandinavia to the Sahara), when planted in one place gave very different results, as regards plant height and yield, in relation to provenience. The seed from the northern points produced taller plants. The following year these differences disappeared. In other words, the influence of the conditions of growth had a definite effect on the properties of the embryo, which disappeared with culture under different conditions.

tained hybrids by crossing the wheat varieties Piper's Tickset and Hopetown. One of these hybrids obtained the gold medal in Scotland in 1848.

Much hybridization work with wheat in the second half of the 19th century in England was done by PATRICK SHIREFF in Scotland, who produced many hybrids between 1856 and 1870. However, these hybrids did not become widely distributed, and only after the rediscovery of MENDEL's Law at the beginning of the 20th Century did the use of hybridization in wheat become widespread. Particularly interesting work prior to the rediscovery of MENDEL's Law was carried out in Australia by the well-known breeder FARRER, whose work, especially on interspecific hybrids of wheat, has not lost significance up till the present.

In the second half of the 19th Century, there was reported the work on wheat hybridization of RIMPAU and HEINE in Germany.

During the past 30 years the situation has fundamentally changed; at the present time the basic method of improving wheat in the principal regions is hybridization. The best present-day wheat varieties have been developed by means of crossing. This applies to the spring wheat variety of Canada, "Marquis," which today occupies almost three-fourths of the entire sown area in North America, and all other spring wheat varieties in Canada (Garnet, Reward, Preston, and others). Sweden, Denmark, Holland, England, Germany, Argentina, Canada, Australia, and South Africa at present cultivate hybrid wheats predominantly.

There arises the question: what shall be crossed, what pairs of parents are the most suitable for obtaining the best combinations?

We thus proceed to the genetics of wheat.

The Genetics of Wheat:— Genetically no other plant has been studied so extensively as wheat. Of the principal publications, we should mention the book of KAJANUS which appeared in 1927, the very valuable work of YU. A. FILIPCHENKO, "Genetics of Soft Wheat" with a supplement by T. K. LEPIN, and the recent Japanese work on plant genetics of MATSUURA, particularly the second edition where there is a rather detailed list of genetic literature from 1900 to 1929.

Most thoroughly investigated has been the genetics of soft wheat and of the species closely related to it, *T. compactum* and *T. spelta.* Much less work has been done on the genetics of the 28-chromosome wheats. Many species of this group, in particular the new species which were found not long ago in Trans-Caucasus and Abyssinia, have hardly been touched genetically. The intraspecific genetics of the 28-chromosome group of wheats is entirely unstudied. Below, we have attempted to give in concise form a summary of all that has been determined up to the present on the genetics of 42- and 28-chromosome wheats, including, for the different characters, the genes that condition them, so far as these are known at the present time.

Of all the 42 characters studied genetically up to the present time, in soft wheats there have been found approximately 200 genes and in 28-chromosome wheats the same characters are determined by approximately 130 genes. These estimates naturally are not exact since in the cases of polymeric characters an exact recognition of the genes is extremely difficult, and accordingly we have only approximate results. In determining the genetics of such characters as vegetative period, the role of external conditions in the manifestation of characters and the numerical relationships in segregation have not usually been considered.

A basic defect in all genetic investigations of wheat just as in other plants, is the element of chance in the selection of materials with which the investiga-

Genotypes of Species of Cultivated Wheats:—
(Based on genetic investigations up to the present time)[1]

Character	Genes: 42-chromosome group	Genes: 28-chromosome group[2]	Authors
Head characters 1. Awnedness and length of awn. Forms awned, awnless, short awned, type *inflatum* with forking curvature and protuberance on the awns (*furcatum*)	1 recessive gene	1 recessive gene	Spillman 1902 Biffen 1905
	2 recessive genes		Love and Craig (1919) with 37 other authors Clark and Hooker 1926, Pero 1929
	4 recessive genes of which 2 are of the first order and 2 of the second order		Clark, Florell, and Hooker 1928
	1 multiple allelomorph: awnless-semiawned-awned		Nilsson-Ehle 1909
	2 dominant genes		A. Howard and G. Howard 1912, Harrington 1922
			Stewart and co-workers 1926-1931
	1 dominant gene G 1 inhibitor I	1 dominant gene F 1 inhibitor H	Raum, 1931
	2-3 unrelated basic recessive genes; 3 genes associated with other characters. Series of gene modifiers	2 unrelated basic recessive genes; 2 genes associated with other characters. Series of gene modifiers	Fortunatova, O. K.
2. Black color of awns	1 dominant gene	1 dominant gene	A. Howard and G. Howard 1912 Sigfusson S. 1932 Love and Craig 1919 Vavilov and Yakushkina 1925
	2 dominant genes		Kadom and Nazareth 1931
3. Smooth awns	1 recessive basic gene 1 or more gene modifiers	1 recessive basic gene 1 or more gene modifiers	Sigfusson 1932
4. Head color	1 dominant gene for red color	1 dominant gene for red color	Tschermak 1901 Biffen 1905 Lewicki 1925 and many other authors
	2 dominant identical genes for red color		Nilsson-Ehle 1911 Malinowski 1914 Love and Craig 1919
	2 dominant genes	1 dominant gene for red color	A. Howard and G. Howard 1912 Kiessling 1914 Barulina
	1 dominant gene for black color	1 dominant gene for black color	Biffen 1905 Engledow 1914 Percival 1921 Kezer and Boyack 1918
	1 dominant gene for black color (G), pleotropic conditioning hairiness of the head	1 dominant gene for black color (G), pleotropic conditioning hairiness of the head	Kajanus 1923 Lewicki 1925
		1 dominant gene for black color, pleotropic, producing head hairiness	Vavilov and Yakushkina 1925 Clark and Smith 1928

[1] Note: 1. This summary is prepared from the basic literature and the best data available to us by T. K. Lepin and O. K. Fortunatova with our corrections and additions.

2. Where a gene has been determined in crosses of wheats of different chromosome numbers, this is indicated in the tables by continuing the data through both the 42- and 28-chromosome columns.

GENOTYPES OF SPECIES OF CULTIVATED WHEATS (*continued*) :—

CHARACTER	GENES: 42-chromosome group	GENES: 28-chromosome group	AUTHORS
		1 recessive gene for black color (in crosses with *T. polonicum*)	BIFFEN 1916 VAVILOV and YAKUSHKINA 1925
5 HAIRINESS OF HEAD	1 dominant gene	1 dominant gene	SPILLMAN 1902 TSCHERMAK 1901 BIFFEN 1905 and 15 other authors
	2 dominant genes	2 dominant genes	A. HOWARD and G. HOWARD 1912
	1 multiple allelomorph hairy, semi hairy, smooth		NILSSON-EHLE 1920
6 LENGTH OF HEAD AND NUMBER OF SPIKELETS (COMPACTNESS)	a) *Genes affecting only head length*		
	Dominant gene C, for short head length (gene determining head type of *T. compactum*)		BIFFEN 1905 NILSSON-EHLE 1900 KAJANUS 1918-1923 ARCISZEWSKI 1924 FILIPCHENKO 1927-1934 and many others
	Dominant gene S increasing head length (gene determining head type of *T. spelta*)		BOSHNAKIAN 1923 KAJANUS 1923 FILIPCHENKO 1929-1934 and other authors
	2 dominant genes S		LEIGHTY and BOSHNAKIAN 1921
	Several genes S		MALINOWSKI 1918-1925
	3 pairs of identical genes E, and 2 gene modifiers, genes K (M_p and M_t)		FILIPCHENKO 1934
	b) *Genes affecting length of head and number of spikelets, increasing them*		
	2 genes L_1 L_2		NILSSON-EHLE 1911 KAJANUS 1923 and other authors
	3 genes L_1 L_2 L_3		ARCISZEWSKI 1924
	3 genes L_1 L_2 L_3		FILIPCHENKO 1924
	2 gene-modifiers of gene L (M_M and M_c); 6 pairs of identical factors P		
		1 gene	ENGLEDOW and HUTCHINSON 1925
	c) *Genes affecting only the number of spikelets, increasing it*		
	2 gene modifiers, gene L		FILIPCHENKO 1934
7. SQUAREHEAD TYPE	Recessive genes cl_1 l_2		NILSSON-EHLE 1911
	1 dominant gene for squareheadedness (Q or M) with recessive gene C		BOSHNAKIAN 1923 ARCISZEWSKI 1924 ILINSKII 1929 RAUM 1929-1930

GENOTYPES OF SPECIES OF CULTIVATED WHEATS (*continued*) :—

Character	Genes: 42-chromosome group	Genes: 28-chromosome group	Authors
	2 recessive genes for squarehead, q and k, forming two types of squareheads: a) Cq—*compactum* b) ck—*vulgare*		FILIPCHENKO 1934
	1 recessive gene r for compactness — *compressum* (cqr)		
8 HEAD BRANCHING	1 recessive gene	1 recessive gene	MEUNISSIER 1918
	Several identical recessive genes		TSCHERMAK 1923 NILSSON-LEISSNER 1925
9. LENGTH OF GLUME TEETH		Several dominant genes (no less than 4 - 5) determining short teeth in *T. durum abyssinicum*	VAVILOV and YAKUSHKINA 1925 VAVILOV, PALMOVA, FLEISCHMANN 1916
		6 pairs of identical genes (*T. durum* subsp. *expansum*) determining short teeth	LEPIN 1930
10. LENGTH OF GLUMES		1 dominant gene determing glume length in *T. polonicum*	BIFFEN 1905 BACKHOUSE 1918 CAPORN 1918 ENGLEDOW 1920-1923
		1 dominant gene P, 4 pairs of gene modifiers (for *T. polonicum*)	LEPIN 1929
	2 dominant genes G 1 recessive gene I with pleotropic effects of genes C_q E L_1 L_2		FILIPCHENKO 1934
11. WIDTH OF GLUMES	1 basic recessive gene and 5 pairs of gene modifiers for strengthening		FILIPCHENKO 1927
12. PRESENCE OF KEEL ON GLUMES		1 dominant gene K	WATKINS 1927
13. WIDTH OF JOINTS OF RACHIS		Several recessive genes	VAVILOV and YAKUSHKINA 1925
14. BRITTLENESS OF RACHIS	1 dominant gene 1 dominant gene B	1 dominant gene 1 dominant gene B	LOVE and CRAIG 1919 RAUM 1931
	1 gene-inhibitor H_b		
Grain characters			
15. GRAIN COLOR: a) red	3 identical dominant genes R_1 R_2 R_3	2 identical dominant genes R_1 R_2	NILSSON-EHLE 1911 GAINES 1917 KAJANUS 1923 and 13 other authors LOVE and CRAIG 1919 HARRINGTON and AAMODT 1923
	2 dominant genes	1 dominant gene	VAVILOV and YAKUSHKINA 1925 BARULINA

Genotypes of Species of Cultivated Wheats (*continued*) :—

<table>
<tr><th rowspan="2">Character</th><th colspan="2">Genes</th><th rowspan="2">Authors</th></tr>
<tr><th>42-chromosome group</th><th>28-chromosome group</th></tr>
<tr><td>b) violet</td><td></td><td>Dominant character, probably 2 genes</td><td>Caporn 1918</td></tr>
<tr><td>16 Grain length</td><td colspan="2">Determined by the same gene as glume length</td><td>Biffen 1905
Engledow 1920
Filipchenko 1927-1934
Miczinski 1930</td></tr>
<tr><td></td><td></td><td>2 unrelated genes for glume length</td><td>Engledow and Hutchinson 1925</td></tr>
<tr><td></td><td></td><td>Dominant gene</td><td>Vavilov and Yakushkina 1925</td></tr>
<tr><td>17. Grain form</td><td></td><td>1 gene dominant for bulge on grain (hump corn)</td><td>Engledow and Hutchinson 1925</td></tr>
<tr><td></td><td></td><td>Dominant gene for wrinkled grain (T. persicum)</td><td>Vavilov and Yakushkina 1925</td></tr>
<tr><td>18. Vitreous grain</td><td>1 basic gene and numerous gene modifiers</td><td>1 dominant gene</td><td>Biffen 1905, 1909
Vavilov and Yakushkina 1925
Bryan and Pressley 1933</td></tr>
<tr><td></td><td colspan="2">2 genes</td><td>Freeman 1917, 1918</td></tr>
<tr><td></td><td colspan="2">Several genes</td><td>Clark and Hooker 1926
Clark, Florell and Hooker 1928</td></tr>
<tr><td></td><td></td><td>2 dominant genes</td><td>Engledow and Hutchinson 1925</td></tr>
<tr><td>Vegetative characters
19. Eligulate character</td><td>Several identical recessive genes</td><td></td><td>Vavilov 1923</td></tr>
<tr><td></td><td>2 identical recessive genes</td><td>1 recessive gene</td><td>Barulina 1933</td></tr>
<tr><td>20. Anthocyanin in auricle of leaf sheath</td><td>1 dominant gene</td><td></td><td>Kajanus 1918-1923</td></tr>
<tr><td></td><td colspan="2">2 identical genes</td><td>Quisenberry 1931</td></tr>
<tr><td>21. Leaf width</td><td colspan="2">1 dominant gene</td><td>Biffen 1905</td></tr>
<tr><td></td><td colspan="2">Several identical genes</td><td>Freeman 1919</td></tr>
<tr><td>22. Hairiness of leaf blade</td><td colspan="2">1 dominant gene</td><td>Biffen 1905</td></tr>
<tr><td></td><td></td><td>Several dominant genes</td><td>Vavilov and Yakushkina 1925</td></tr>
<tr><td>23. Waxy layer on stems and leaves</td><td colspan="2">Dominant genes</td><td>Tschermak 1923
Miczinski 1907</td></tr>
<tr><td></td><td colspan="2">1 dominant gene</td><td>Watkins 1927</td></tr>
<tr><td></td><td></td><td>Recessive gene</td><td>Miczinski 1930
Yakubtsiner 1932</td></tr>
<tr><td>24. Hairiness of nodes</td><td>1 dominant gene</td><td></td><td>Love and Craig 1924
Gaines and Carstens 1926</td></tr>
<tr><td></td><td></td><td>Several dominant genes (T. persicum)</td><td>Vavilov and Yakushkina 1925</td></tr>
<tr><td>25. Anthocyanin in straw</td><td>Dominant gene
1 dominant gene</td><td></td><td>Schribaux 1907
Jenkin 1925</td></tr>
<tr><td>26. Straw length</td><td colspan="2">Several identical genes</td><td>Freeman 1918
Clark and Hooker 1926
Stewart and co-workers 1926-1929
Harrington 1925</td></tr>
</table>

GENOTYPES OF SPECIES OF CULTIVATED WHEATS (*continued*) :—

CHARACTER	GENES: 42-chromosome group	GENES: 28-chromosome group	AUTHORS
	1 dominant gene		YAMASAKI and HATANO 1930
27. CLUB WHEAT CHARACTER	1 dominant gene		VILMORIN 1913 ENGLEDOW and WADHAM 1925 WINGE 1924
	1 dominant gene D		STEWART and BISHOFF 1931
	1 gene-inhibitor I		NIEVES 1930 TINGEY 1931 THOMPSON 1928 CLARK and QUISENBERRY 1929 GOULDEN 1926
	2 dominant genes		WALDRON 1924 CLARK and HOOKER 1926 STEWART and TINGEY 1928 STEPHENS 1927
	2 dominant genes 1 gene inhibitor		CHURCHWOOD 1932
	1 recessive gene		NEETHLING 1918
28. STRAW THICKNESS	Several identical genes		TSCHERMAK 1901
29. SOLIDNESS OF STRAW UNDER HEADS	1 recessive gene		BIFFEN 1905 STOLL 1911 KAJANUS 1923
	Several identical genes		TSCHERMAK 1923 KIHARA 1924
	1 multiple allelomorph		ENGLEDOW 1920, 1923 ENGLEDOW and HUTCHINSON 1925
	Several dominant genes (*T. persicum*)		VAVILOV and YAKUSHKINA 1925
30. FORM OF GROWTH	1 gene		PERCIVAL
31. COLOR OF COLEOPTILE: *a*) Violet	1 dominant gene		GOULDEN, NEATBY and WELSH 1928
b) Albinism	3 recessive genes	2 recessive genes	SMITH and HARRINGTON 1929 HARRINGTON and SMITH 1928
	5 pairs of identical genes		SAPEHIN, L. A. 1932
Biological characters 32. WINTER AND SPRING HABIT (under definite environmental conditions)	Winter type dominant		SPILLMAN 1909 AAMODT 1923 NILSSON-EHLE 1915
	Spring type dominant		OLSON and others 1920 COOPER 1923 NILSSON-LEISSNER 1925
	2 recessive genes for winter type		GAINES 1928 STEWART 1931
	Several identical recessive genes for winter type. Segregation is frequently very complicated; forms occur which are earlier than the parents; numerical relationships are not referable to a sim-		VAVILOV and KUZNETSOVA 1922

GENOTYPES OF SPECIES OF CULTIVATED WHEATS (*continued*) :—

CHARACTER	GENES: 42-chromosome group	GENES: 28-chromosome group	AUTHORS
	ple scheme. There is reported occurrence of plants in F_3 and F_4 that are unable to tiller		
33. EARLY MATURITY (presence under definite environmental conditions; findings are related to environmental conditions)	1 dominant gene	1 dominant gene	BIFFEN 1905 FLORELL 1924 CLARK 1924
	Several identical genes		NILSSON EHLE 1911 FREEMAN 1918 THOMPSON 1918-1921 BRYAN and PRESSLEY 1921 STEPHENS 1927 CLARK and HOOKER 1926 HARRINGTON 1925
34. WINTER RESISTANCE (under definite environmental conditions)	Several identical genes		NILSSON-EHLE 1911-1913 SHAFER 1923 ÅKERMAN 1922 MAYER and AAMODT 1927 CRÉPIN, ALABOUVETTE and CHEVALIER 1930 QUISENBERRY 1931
35 LODGING	1 recessive gene 2 recessive genes		SPILLMAN 1905 A HOWARD and G. HOWARD 1915
	Several identical genes		NILSSON-EHLE 1913
36. SHATTERING	2 dominant genes		A HOWARD and G. HOWARD 1912 LEWICKI 1928
	1 recessive gene		MICZINSKI 1930
37. IMMUNITY	1 dominant gene		
a) From *Puccinia glumarum*	1 recessive gene Several gene modifiers		ISENBECK 1931 BIFFEN 1905-1907 ARMSTRONG 1922 WATKINS 1927 ISENBECK 1931 VAVILOV 1919
	Several identical genes		NILSSON-EHLE 1911 ENGLEDOW and HUTCHINSON 1925 PESOLA 1924 VAVILOV and YAKUSHKINA 1925 HUBERT 1932, ISENBECK 1931 RUDORF 1930-1933
b) From *Puccinia triticina*	1 dominant gene		ISENBECK 1931 MAINS, LEIGHTY and JOHNSTON 1926 WATERHOUSE 1930
	1 recessive gene		BACKHOUSE 1917 MAINS and others 1926
	Several recessive genes		VAVILOV and YAKUSHKINA 1925
c) From *Puccinia graminis tritici*	1 recessive gene		POLE EVANS 1911 GOULDEN, NEATBY and WELSH 1928, HARRINGTON and AAMODT 1928 HAYES, STAKMAN and AAMODT 1925

GENOTYPES OF SPECIES OF CULTIVATED WHEATS (*concluded*) :—

CHARACTER	GENES: 42-chromosome group	GENES: 28-chromosome group	AUTHORS
	1 dominant gene		MELCHERS and PARKER 1922, QUISENBERRY 1931, WATERHOUSE 1930
	2 recessive genes	1 recessive gene	HAYES and AAMODT 1923
		2 recessive genes	CLARK and SMITH 1928 WALDRON 1921
	Several dominant and recessive genes		CLARK and AUSEMUS 1928 SMITH 1927 HARRINGTON 1925 HAYES, AAMODT, and STEVENSON 1927 MCFADDEN 1925 GOULDEN, NEATBY and WELSH 1928 QUISENBERRY 1931 STEWART 1926-1929 WALDRON 1921, 1926
	2 dominant genes 1 gene inhibitor		NEATBY and GOULDEN 1930
	1 basic dominant gene and several gene modifiers		PUTTICK 1921 QUISENBERRY 1931
d) From *Erysiphe graminis*		Several dominant genes	VAVILOV 1913-1919 VAVILOV and YAKUSHKINA 1925
	Several recessive genes		
e) From *Tilletia tritici*	Several recessive identical genes		GAINES 1920, 1925 NIEVES 1930 KNORR 1929
	Several dominant genes		GIESEKE 1929 BRIGGS 1926-1933 GAINES and SINGLETON 1926
	1 recessive gene		CHURCHWARD 1931, 1932 BRIGGS 1934 THATCHER 1921
f) From *Ustilago tritici*	1 recessive gene		PIEKENBROCK 1927 GREVEL 1930
	Several identical genes		OLSON 1920
g) From *Septoria tritici*	1 recessive gene		MACKIE 1929
h) From *Fusarium*	Series of genes		CHRISTENSEN 1927
38. REDUCTION DIVISION	Several pairs of recessive gene-disorganizors		SAPEHIN, L. A. 1933
39. FORMATION OF DIPLOID GAMETES	Several pairs of genes governing the formation of giant pollen grains		SAPEHIN, L. A. 1933
40. FORMATION OF CROSS-WALLS IN DIADS AND TETRADS	Several pairs of genes governing the absence of cross-walls between daughter nuclei		SAPEHIN, L. A. 1933
41. ABSENCE OF CONJUGATION OF PARASYNAPTIC TYPE	Several pairs of recessive genes governing the absence of conjugation		SAPEHIN, L. A. 1933

tors work. Ordinarily all genetic investigations have been carried out on materials which by chance came to be at the disposal of the investigator, without consideration of the vast ecological-geographical diversity which actually occurs in wheat species. Many authors, particularly in the past, hardly made much distinction even between wheat species (see, for example, FREEMAN). There

is some justification for this since the differential botanical-geographical investigations of wheat species on a world scale was first undertaken within the past ten years, while the sharp differentiation of species according to chromosome numbers has been only recently recognized. Extensive materials from the regions where wheat was first cultivated, such as Abyssinia, Afghanistan, India, and the Mediterranean region, as we know, were lacking in work of geneticists and breeders, and hence, all the findings of present-day genetics of wheat must still be considered as only preliminary. The comparative genetics of wheat species has hardly been worked upon.

Nevertheless, at present we have a series of genetic findings of prime significance which must be regarded as basic in practical breeding.

Pleotropic Effects of Genes in 42-chromosome Wheats:—

Gene	Character affected	Authors
1 Gene for compactness C	1) Length of head 2) Length of head 3) Length of head 4) Length of head 5) Number of grains 6) Length of awns 7) Length of straw	Sapehin, L. A. and co-workers 1916-1922 Gaines 1917
2 Gene for speltoid character S	1) Length of head 2) Brittleness 3) Milling difficulty 4) Compactness of glume 5) Narrowness of head	Kajanus 1923 Nilsson-Leissner 1925 Filipchenko 1934
3 Genes for elongate head L	1) Length of head 2) Number of spikelets 3) Length of glume 4) Length of grain	Nilsson-Ehle 1911 Kajanus 1923 Arciszewski 1924 and a number of other authors Filipchenko 1934
4. Gene-modifiers for gene M_P and M_C and identical factors of head form P	1) Length of head 2) Number of spikelets	Filipchenko 1934
5. Genes for head form E	1) Length of head 2) Length of glumes 3) Length of grain	Filipchenko 1934
6 Gene for squarehead, *compactum* type Q	1) Compactness of upper part of head 2) Height of plant 3) Length of glumes 4) Length of grain	Filipchenko 1934
7. Gene for squarehead, *vulgare* type K	1) Compactness of upper part of head 2) Height of plant	Filipchenko 1934
8. Gene for black head color G	1) Black head color 2) Head hairiness	Kajanus 1923

First of all, we know of genetic series of qualitative characters which, in their inheritance, conform to a simple Mendelian scheme, showing clear-cut segregation that follows the ordinary mono-, di-, tri-hybrid scheme. Such are the characters of awnedness, awnlessness, smooth awns, grain color, head color, hairiness of heads, and presence or absence of ligules. Moreover, some of these characters have considerable significance for practical breeding.

In these investigations we encounter an interesting rule which must be confirmed by further investigation, namely that hexaploid wheats, *i.e.*, types of soft wheat with 42 chromosomes, are characterized by a greater number of genes than the group of hard wheats with 28 chromosomes for any given character. For example the presence of ligules in soft wheats is governed by two genes, while in hard wheats by only one. The same thing may be said with reference to head color: in soft wheats there are two dominant genes de-

termining red color of the heads, and in hard wheats only one. This also applies to grain color.

Considering multiple assortments of chromosomes, and the chance that they may be duplicated, we have the possibility of the presence of pairs of genes in hexaploid wheats which may be associated with homologous chromosomes. In any case these facts on the genetic differences in behavior of different chromosomal groups of wheats have great interest and demand further study in view of their practical and theoretical significance. It is also necessary to bring into the investigations the group of einkorn wheats, since they show great intraspecific diversity of form.

Recent investigations of V. A. PODDUBNA in the cytological laboratory of the Institute of Plant Industry (1935) have shown that within the 28-chromosome wheats chromosomes do not repeat one another, *i.e.*, there is no autoploidy but instead, alloploidy. This fact has great importance for wheat genetics. The soft wheats require further study.[70]

Pleotropic Effects of Genes in 28-chromosome (tetraploid) Wheat:—

GENE	CHARACTER AFFECTED	AUTHORS
9. BASIC GENE FOR POLISH WHEAT P	1) Length of glumes 2) Length of head 3) Number of spikelets 4) Length of grain 5) Length of awn 6) Length of teeth 7) Hairiness of head 8) Color of head and 9 other secondary characters	LEPIN 1932 BACKHOUSE 1918 ENGLEDOW 1920-1923
10. GENE FOR BLACK HEAD COLOR (IN *T. persicum*)	1) Black head color 2) Hairiness of head	VAVILOV and YAKUSHKINA 1925

Quantitative characters such as head length, number of spikelets, height of plant, length of glumes, and size of grain are ordinarily determined by several genes which may either be identical (polymerism) or distinct. Investigations of recent years permit us more and more to consider that there is a *reciprocal relationship between genes:* in this case if a single character is determined by several genes, their combined effect is not always their arithmetical mean.

The same refers to physiological characters, the majority of which are determined by several genes.

In a number of cases, for example in relation to immunity from stripe, leaf, and stem rust, there is observed a rather clear polymerism. NILSSON-EHLE, in his classic investigations on wheat, came to the conclusion that immunity from or susceptibility to stripe rust, as well as several other characters, for example cold-resistance, are determined by several identical genes. He was not able to determine the exact number of genes. We have come to the same conclusion with respect to immunity of wheat from powdery mildew and stripe rust.

Likewise, investigations of *physiological* characters such as spring and winter habit of life, clearly show not only the occurrence of polymerism, but also the presence of dissimilar genes. In the light of the study of development by stages, on the relationship between given stages of development and external conditions, such a conclusion appears to be natural. Despite the older assumption of BIFFEN and other authors on the occurrence of simple Mendelian re-

[70] Unpublished data. Reported on the basis of examination of cytological preparations kindly demonstrated to us by V. A. PODDUBNA.

lationships in the phenomenon of immunity, recent investigations have disclosed that this is much more involved, especially since intraspecific parasites often are now known to be more complicated than was formerly recognized. Genetic investigations of physiological and quantitative characters show the presence of a large number of genes determining varietal differences. The presence in nature of a great many small heritable differences in length of head, length of seed, and size of leaves testifies to the great number of corresponding genes.

Linked Genes in Wheat:—

Genes	Authors
Gene for awnless N and gene for speltoid S; % crossing 35%	Kajanus 1926; Nilsson-Leissner 1925; Meyer 1925; Nilsson-Ehle 1927; Watkins 1929; Filipchenko 1934
Gene for awnless N and gene for squarehead q; % crossing 35%	Filipchenko 1934
Gene for awned A and gene for awned [Sic] T; % crossing 35%	Stewart 1926-1928
Reverse linkage	
Gene for hairiness H and gene for red color B; Gamete ratio 1 : 15 : 15 : 1	Kajanus 1923
Gene for black color B, not associated with hairiness, and gene for hairy H; Gamete ratio 1 : 3 . 3 · 1	Engledow 1914
Almost absolute linkage	
Gene for hairy nodes and gene for awned	Love and Craig 1923
Type *polonicum* and white head: Violet color of grain, white color of head, black color of awn, and hairy head. Short awned and *Triticum turgidum abyssinicum* type	Vavilov and Palmova

The number of these must be very large in relation to such characters as immunity, since in only a single form of stem rust, that of wheat (*Puccinia graminis tritici*), at the present time there have been separated out some 150 physiologic races which differ with respect to the different wheat varieties.

Nevertheless, for all these characters, in hybridization there is clear-cut segregation. The cases of "absorbed characters," for example in crossing Persian wheat with hard wheat, where the beak-like glume teeth of the parental forms do not appear in the 2nd, 3rd, and 4th generations,[71] may possibly be explained by the presence of a large number of genes, although this fact requires further investigation.

In any case, the number of genes distinguishing species and varieties of wheat must be very great, numbering into thousands. This is indicated by the

[71] This has been seen in our experiments. See N. Vavilov and O. Yakushkina: "On the phylogeny of wheat." (1925).

number of wheat species, the occurrence of highly differentiated species, the individuality of different geographic groups, and the great variety of forms within species, as has been brought out in the foregoing table of heritable variations within species. If we adopt the conception of HARLAND that different species do not have identical genes (which does not appear to us very probable)[72] this would lead us to a conception of a still greater number of wheat genes.[73]

A number of wheat genes appear to have pleotropic effects. Thus the investigations of YU. A. FILIPCHENKO and T. K. LEPIN have shown that a number of genes simultaneously affect the length of heads, length of glumes, length of grains, number of grains, and even length of awns and straw. Genes for head length in a number of crosses also determine the number of spikelets, length of glumes, and length of grains. In *T. persicum,* as we have shown, the black color of heads is inseparably associated with hairiness of heads. In the Polish wheat (T. K. LEPIN) a whole species complex is determined by the pleotropic effects of single genes. Single genes condition the consistency of the glumes and the size of organs.

Along with pleotropic effects of genes there is also, no doubt, linkage of genes. YU. A. FILIPCHENKO demonstrated the linkage of genes for awnlessness and squarehead, and genes for awnlessness and speltoid type. KAJANUS showed an antagonism between gametes carrying the genes for hairiness and color of heads (gamete ratio 1:15:15:1). Evidently linkage is more frequent in species with 28 chromosomes than in those with 42, which necessarily follows from the chromosome theory of heredity.

Map of First Chromosome of Soft Wheat:—

q	35%	N	33%	S
Gene for squarehead		Gene for awnless		Gene for speltoid (according to FILIPCHENKO 1934)

In connection with a number of characters, in addition to the basic genes, there have been demonstrated the effects of gene modifiers. Such genes have been found in relation to length and form of glumes; in Polish wheat gene modifiers have been demonstrated associated with vitreousness of the grain and looseness of the head.

With regard to recessiveness and dominance in wheat, this has been clearly shown for a number of characters, and is constantly being used in breeding. Awnedness, as we know, in a great majority of forms, appears to be a recessive character; black and red head colors are dominant over white; red grain is dominant over white; hairiness of head is dominant over smooth glumes. With respect to other characters, particularly quantitative ones, the relationships are more complicated. A character which is dominant in one form or variety may be recessive in others. This situation is particularly frequent with respect to immunity from fungus diseases. In determining dominance and recessiveness of physiological characters, it is particularly necessary to consider the conditions under which the plant develops.

In comparison with *Drosophila,* and even with corn, wheat has been studied comparatively less. The large number of chromosomes in soft and hard wheats makes it very difficult to construct their chromosome maps. This phase of the

[72] S. E. HARLAND: "Genetic conception of species." Dokl. Akad. Nauk. Nov. 1933.
[73] In his latest work, HARLAND, in the Journal of Genetics, Vol. 30, No. 3, 1935, has found homologous genes for blossom color in Asiatic and American cottons.

work requires extensive additional experimental materials. The investigation of species with 28 chromosomes deserves particular attention in this connection. The fundamental problem here appears to be a comparative study of the genetics of the different species.

Selection of Parental Pairs in Crossing:— The great diversity of wheat forms discovered in recent years underlies the selection of the most valuable combinations for solving practical problems in breeding. The practical breeder in the past and up to the present has had to do primarily with intraspecific hybridizations. The majority of the valuable varieties have been developed by crosses between different forms of soft wheats, or, in a few cases, between closely related species such as *T. compactum* and *T. spelta.*

Despite hundreds of genetic investigations, unfortunately the question of the selection of parental pairs has hardly been studied. Up to the present there has been no theory of the selection of parents, with the exception of the use of related species. Breeders have used for crossing those varieties which, from visual inspection, have appeared to have interesting characters. There have been no rules in the selection of parents, and each breeder has gone his own way.

The colossal works on breeding of wheat throughout the world have been separate and disconnected. Up to the present there has been no precise appraisal of the world breeding work even on the most important cereal crop.

We are attempting to evaluate the world work. This is not easy; most of the varieties produced by breeding have been developed by private firms with their customary secrecy. In this connection it is better to deal with the work of the Experiment Stations, although even here the work is far from scientifically ideal. Even the varietal nomenclature of wheat up to the present has been a jargon; in few cases has the basic geographic origin of the materials been indicated. Until recently the sources of varieties for breeding nurseries in the Experiment Stations have been seed firms, with the well-known German firm Haage and Schmidt, for example, supplying assortments for all stations. Many of our own breeding institutions began with such material.

In order to explain the method of obtaining the most successful combinations of wheat, we will consider 50 of the best varieties which have been developed by hybridization in different regions, and for which we have well documented genealogies. Fortunately, for many of the most valuable varieties, these genealogies are available.

We begin with *Canada.*

In the following tables are given the pedigrees of the best Canadian varieties, *viz.:* "Marquis," "Preston," "Prelude," "Garnet," "Reward." The variety Marquis appears to be the most outstanding accomplishment in world breeding, having unusual qualities for the conditions of Canada and the northern United States, with fine round grain having a high production of flour of excellent quality, stiff straw, resistance to stripe rust, non-shattering, comparative drought resistance under the conditions of Canada, and sufficient earliness for the basic regions of its cultivation. At present Marquis occupies about 70% of the entire acreage under wheat in Canada, estimated at eleven million hectares. Another new Canadian variety, Reward, developed by NEWMAN in Ottawa, is distinguished from Marquis by its greater earliness. On this variety has been based the extension of wheat to the northward in Canada, and it occupies at present about 10% of the acreage under wheat in this region.

As may be seen, the pedigrees of the Canadian improved varieties are very complicated. Forms from different geographic areas have had particular value

Pedigrees of Hybrid Varieties of Soft Wheats of Canada:—

(Developed by W. and Ch. Saunders and Newman)

Marquis, var. *lutescens*:—

Hard Red Calcutta × Red Fife (1892)
(India) (Galicia)

↓

Marquis (1903)

Ruby (1917):—

Gehun × Onega
(Himalayas) (Archangel)

↓

Early Riga

↓

Downy Riga × Red Fife

↓

Ruby (1917)

Prelude var. *pseudo-hostianum*:—

Ladoga × White Fife
(SSSR) (Galicia)

↓

Alpha × Hard Red Calcutta
(India)

↓

Frazer × Gehun
(Himalayas)

↓

Prelude (1913)

Preston, var. *erythrospermum* (1896):—

Ladoga × Red Fife
(SSSR) (Galicia)

↓

Preston (1896)

Garnet, var. *lutescens* (1926):—

Ladoga × Red Fife (1888) → Preston → Preston A

Onega × Gehun (1891)
(SSSR) (Himalayas) → Early Riga → Riga M (1905)

Preston A × Riga M (1905)

↓

Garnet
Increase begun in 1926

Reward, var. *lutescens*:—

Ladoga × Red Fife (1888)
(SSSR) (Galicia)

↓

Alpha × Hard Red Calcutta (1892)
(India)

↓

Fraser × Gehun (1892)
(Himalayas)

↓

Prelude

Hard Red Calcutta × Red Fife (1903)
(India) (Galicia)

↓

Marquis (1912)

Prelude × Marquis (1912)

↓

Reward

Pedigree of the Hybrid Wheat Variety "Novinka":—

(Developed by V. E. Pisarev, All-Union Institute of Plant Industry)

Ladoga × Red Fife
(SSSR) (Galicia)

↓

Alpha × Hard Red Calcutta
(India)

↓

Frazer × Gehun
(Himalayas)

↓

Prelude

Ladoga × Red Fife
(SSSR) (Galicia)

↓

Preston

Preston × Prelude

↓

Novinka

Pedigrees of Hybrid Varieties of Wheat of the USA:—

Hope, 1925 (breeder McFadden) :—

Yaroslav emmer (*T. dicoccum*) × Marquis (*T. vulgare*)
↓
Hope
H-44
(Resistant to *Puccinia graminis* f. *tritici*, and to loose and covered smut; characterized by high milling quality)

Marquillo, 1926 (breeder Hayes) :—

Marquis (*T. vulgare*) × Iumillo (*T. durum*)
↓
Marquillo

Hybrid Soft Wheats:—

Ceres, 1925 (breeder Waldron) :—

Marquis × Kota (SSSR)
↓
Ceres

Minturki, 1919 (breeder Hayes) :—

Odessa (SSSR) × Turkey (SSSR)
↓
Minturki

Minhardi, 1920 (breeder Hayes) :—

Odessa (SSSR) × Turkey (SSSR)
↓
Minhardi

Pedigrees of Hybrid Wheat Varieties of Australia (Soft Wheats):—

Bunyip (breeder Farrer) :—

Purple Straw (N. America) × Improved Fife (Galicia) → Rymer
King's Jubilee × Unname (Australia) → Maffra
Rymer × Maffra
↓
Bunyip

Federation (breeder Farrer) :—

Improved Fife (Galicia) × Etawah (India)
↓
Yandilla × Purple Straw (USA)
↓
Federation

Aurora (breeder Farrer) :—

Improved Fife (Galicia) × Etawah (India)
↓
Yandilla × Purple Straw (California)
↓
Federation
Selected from it
↓
Hard Federation

Saskatchewan Fife (Canada) × Improved Fife (Galicia)
↓
Hornblende × Blount's Lambrigg Selection
↓
Hybrid × Purple Straw Tuscan (Mediterranean)
↓
Cleveland

Hard Federation × Cleveland
↓
Hybrid × Sands (Individual selection from Federation)
↓
Aurora

Florence (breeder FARRER) :—

White Naples (Italy) × Improved Fife (Galicia)
↓
Unnamed × White Naples
↓
Unnamed

Improved Fife × Eden
↓
Unnamed

Unnamed × Unnamed
↓
Florence

Major (breeder PAI) :—

Improved Fife (Galicia) × Etawah (India)
↓
Yandilla × Purple Straw (N. America) Complex hybrid
↓
Federation

Purple Straw (N. America) × Fife Indian (India)
↓
Wallace

Federation × Wallace
↓
Major

Thew (breeder FARRER) :—

Sinew × Improved Fife (Galicia)
↓
Unnamed

Improved Fife (Galicia) × Hussar (USA)
↓
Unnamed

Unnamed × Unnamed
↓
Selection from Blount's Lambrigg × Unnamed
↓
Thew

Warden (breeder PAI) :—

Quartz × Ward's White
↓
Unnamed × Red Bordeaux (France)
↓
Warden

Yandilla King (breeder R. MARSHALL) :—

Improved Fife (Galicia) × Etawah (India)
↓
Yandilla × Silver King
↓
Yandilla King

Gallipoli (breeder A. RICHARDSON) :—

Improved Fife (Galicia) × Etawah (India)
↓
Yandilla × Silver King
↓
Club Head × Yandilla King
↓
Gallipoli

Jonathan (breeder FARRER) :—

Fife (Galicia) × Hussar (USA)
↓
Unnamed × Indian (India)
↓
Jonathan

Carrabin:—

Fife × Hussar
(Galicia) (USA)
↓
Unnamed × Indian G
(India)
↓
Jonathan × Zaff
(India)
↓
Unnamed × Powers Fife
(USA)
↓
Unnamed × Powers Fife
↓
Cedar

White Naples × Improved Fife
↓
Unnamed × White Naples
↓
Unnamed

Improved Fife × Eden
(Galicia)
↓
Unnamed

Unnamed × Unnamed
↓
Florence

Cedar × Florence
↓
Carrabin

Merredin:—

White Naples × Improved Fife
(Italy) (Galicia)
↓
Unnamed × White Naples
↓
Unnamed

Improved Fife × Eden
↓
Unnamed

Unnamed × Unnamed
↓
Florence × Gluyas Early
(Egypt)
↓
Merredin

Pedigrees of Hybrid Wheat Varieties of Italy (Soft Wheats):—

Carlotta Strampelli, 1905 (breeder STRAMPELLI):—

Shireff × Bordeaux
(Scotland) (France)
↓
Rieti × Massy
(Italy)
↓
Carlotta Strampelli

Ardito Strampelli, 1916 (breeder STRAMPELLI):—

Squarehead × Zeluhd
(England) (Holland)
↓
Spyk × Squarehead
(England)
↓
Wilhelmina × Rieti
(Holland) (Italy)
↓
Ibrido 21 × Akagomughi
(Japan)
↓
Ardito Strampelli

Zara (breeder STRAMPELLI):—

Noé × Blé Shireff
(France) (Scotland)
↓
Gros bleu × Chiddam d'automne
(England)
↓
Hâtif Inversable × Rieti
(France) (Italy)
↓
Zara

Varrone (breeder Strampelli) :—

Rieti × Wilhelmina Tarwe
(Italy) (Holland)
↓
Varrone

Dante (breeder Strampelli) :—

Rieti × Wilhelmina Tarwe
(Italy) (Holland)
↓
Hybrid × Akagomughi
(Japan)
↓
Dante

Fausto Sestini (breeder Strampelli) :—

Rieti × Wilhelmina Tarwe
(Italy) (Holland)
↓
Hybrid × Akagomughi
(Japan)
↓
Fausto Sestini

Mentana (breeder Strampelli) :—

Rieti × Wilhelmina Tarwe
(Italy) (Holland)
↓
Hybrid × Akagomughi
(Japan)
↓
Mentana (Differs from the variety Ardito in not shattering)

Pedigrees of French Wheats Produced by the Vilmorin Firm (Soft Wheats) :—

Bon Fermier (var. *lutescens*) 1904 :—

Noé × Blé Shireff
(France) (Scotland)
↓
Gros bleu × Blé seigle
(France)
↓
Bon Fermier

Hâtif Inversable (var. *lutescens*) 1908 :—

Noé × Blé Shireff
(France) (Scotland)
↓
Gros bleu × Chiddam d'automne
(England)
↓
Hâtif Inversable

Grosse tête (var. *lutescens*) 1899 :—

Browick × Chiddam d'automne
(England) (England)
↓
Grosse tête

Dattel (var. *alborubrum*) 1884 :—

Chiddam d'automne × Prince Albert
(England) (England)
↓
Dattel

Bordier (var. *albidum*) 1890 :—

Prince Albert × Noé
(England)
↓
Bordier

Massy (var. *lutescens*) 1902 :—

Square Shireff × Bordeaux
(Scotland) (France)
↓
Massy

Blé des Alliés (var. *albidum*) 1917 :—

Parsel × Massy × Japhet × Parsel

Blé de la Paix (var. *milturum*) 1919 :—

Noé × Blé Shireff (Scotland)
↓
Gros bleu × Chiddam d'automne — Bordeaux × Champlan
↓ ↓
Hâtif Inversable × Chambor
↓
Blé de la Paix

Vilmorin 23 (var. *lutescens*) 1923 :—

Melbor × Grosse tête × Japhet × Parsel

Vilmorin 27 (var. *lutescens*) 1927 :—

Chiddam (England) × Prince Albert (England) — Noé × Shireff — Noé × Shireff
↓ ↓
Gros bleu × Chiddam — Gros bleu × Blé seigle
↓ ↓ ↓
Dattel × Japhet × Parsel × Hâtif Inversable × Bon Fermier
↓
Vilmorin 27

Pedigrees of Hybrid Wheat Varieties from Sweden (Soft Wheats) :—

Pansar III, 1922 (Svalöv) :—

Landweizen (Local Swedish) × Squarehead (England)
↓
Grenadier × Kotte Landweizen (Local Swedish)
↓
Pansar III

Extra Squarehead III (Svalöv) :—

Local Swedish × Squarehead (England)
↓
Grenadier × Extra Squarehead I
↓
Grenadier × Extra Squarehead II
↓
Extra Squarehead III

Thule II (Svalöv) :—

Local Swedish × Squarehead (England)
↓
Pudel × Local Swedish
↓
Thule I
↓
Thule II

Svea (Svalöv) :—

Local Swedish × Squarehead (England)
↓
Pudel × Swedish local
↓
Thule I × Swedish local × Pudel
↓
Svea

Pedigrees of Hybrid Wheat Varieties of Argentina (Soft Wheats) :—

38 MA:—

Barleta (Spain) × Chino (China)

H. 33 (breeder KLEIN) :—

Ardito × Vencedor
(Italy)
(Strampelli hybrid involving Japanese wheats)

H. 32 (breeder KLEIN) :—

Ardito × Record
(Italy)

H. 31 (breeder KLEIN) :—

Ardito × IV h
(Italy)

H. 40 (breeder KLEIN) :—

Barleta × Chino
↓
38 MA × San Martin
↓
H. 40

San Martin:—

Favorito × Americano 25

Vencedor:—

Record × Barleta
(Spain)

in the creation of the Canadian varieties, including our Siberian and European early-maturing spring varieties, as Onega and Ladoga, and early-maturing forms from northwestern India. Also in their formation have been used European and Galician varieties. The pedigrees of the Canadian varieties bring out clearly the complicated process in creating good varieties which necessitates a complex of repeated crossings. The genealogy of Marquis began in 1892; the breeding was started by SAUNDERS the father and completed by SAUNDERS the son, with the variety Marquis appearing in 1903 after 10 or 11 generations.

Unfortunately, even for the first-class variety "Marquis" the pedigree is incompletely known, since we do not have full information on the nature of the original parental Indian and Galician forms. We do not know how segregation proceeded, or the number of plants involved in the work.

Nevertheless the Canadian work clearly shows that noteworthy success may follow the use of very distinct geographic races within soft wheat species, the selection of different ecological types for crossing, and strict selection for grain quality. This last is particularly characteristic of Canada, where wheat is developed mainly for a world market. Canada has evidently obtained its high quality grain from Indian varieties.

A similar example of our own is the development by V. E. PISAREV of the northern wheat variety "Novinka" which is adapted to culture up to 65.5° N. Lat. (Solovka), the creation of which involved in part the use of the Canadian varieties "Preston" and "Prelude."

In the *United States of America* a number of valuable winter forms have been obtained by crossing our Crimean and Ukrainian varieties among themselves. A number of new varieties have been recently developed through the use of interspecific hybridization, which will be discussed later.

In the breeding of the *United States* a decisive role has been played by our Ukrainian and Crimean winter forms. The basic wheats in mass culture in the United States are our ordinary Ukrainian forms or hybrids between them. Such, for example, are "Minturki" and "Minhardi." Some of the American varieties have even retained their Russian names, such as "Kharkov."

Particular interest attaches to the breeding practice of *Australia*. Probably no region in the world in recent times has carried out such extensive hybridization work as Australia.

In its dry climate Australia resembles the Soviet Union. Yields there are ordinarily lower than those in our region. Drought, rust, smut, and a short vegetative period—these are the basic problems which have underlain the breeding work in Australia. This has led to a selection from the world diversity of forms. The lack of suitable local varieties for these dry conditions necessitated crossing, and a search for the necessary components. Much, in particular, was done at the end of the 19th century by the Australian breeder FARRER. His initial materials were primarily from United States, Canada, and India, the larger regions producing wheat. Literally thousands of different crosses were made, and these resulted in the production of hundreds of varieties. For the most part Australia has fairly satisfactory documentation of its breeding work.

In looking over the numerous pedigrees of Australian hybrid wheats,[74] we can once again see the decisive role in the use of suitable types of different geographic races. We again see here the participation of Indian early maturing forms, Russian forms, and Mediterranean varieties of soft wheat. One of the noteworthy varieties, "Federation," which was developed by FARRER in 1901, and still has significance for us, was obtained by crossing Galician, Indian, and Californian wheats. Still more complex was the production of another spring variety by FARRER, Aurora, which does very well in Sweden and in the northern part of our country. In its creation, there took part Federation, the variety Cleveland, a complicated American wheat hybrid, and the variety Sands, one of the lines from Federation.

As we know, the selection of two parental forms does not guarantee our obtaining a desirable variety. Frequently in the formation of improved varieties, there participate four or more initial types. There are combined diverse types from remote regions which eventually give desired combinations. Unfortunately we have no data on the number of plants, the extent of the work, or the process of segregation, to enable us to follow the whole process of the creation of these varieties. In any case, however, it is very clear that the best improved varieties of Australia have been the result of complex combinations of different geographic types.

* * * * *

In *Italy* the greatest interest attaches to the hybridization work of the Institute headed by the eminent breeder STRAMPELLI, who created a number of excellent varieties which today are widely cultivated, not only in Italy but also in neighboring countries. Particularly outstanding is his variety Ardito. From Italy this variety has entered Argentina, Chile, and France, and today occupies millions of hectares. Its one serious defect is its shattering. Its pedigree includes an English wheat of the squarehead type and an Italian local form of the Rieti type, while a decisive role in Ardito's formation was played by the Japanese variety Akagomughi, which has an oriental appearance, is low growing, with bright yellow color, and shatters easily, a characteristic of Japanese wheats. The role of Japanese varieties is an outstanding feature of recent Italian breeding.

The firm Vilmorin and André in *France* carried extensive hybridization work with wheat for about 60 years, and this is quite well documented as regards the breeding process. In the nature of components in the formation of the bred varieties of France, as we may see from the foregoing table, a decisive role was played, along with local varieties, by the English squareheads. The Russian wheats also took some part in the formation of the improved French varieties.

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[74] MCMILLAN, J. R. Varieties of wheat in Australia. Council for Scientific and Industrial Research, Bull. 72, Melbourne, 1933.

The greatest accomplishments of the Vilmorin breeders were the varieties Vilmorin 23 and Vilmorin 27. Unfortunately this work has given us no records of the process of segregation, and even the original varieties used were not identified by geographic data or ecological characteristics.

The *English* improved wheat varieties of recent times have been created mainly with the use of the old squareheads crossed with Russian varieties. Thus BIFFEN produced the variety "Little Joss" by crossing "Squarehead Master" with the Russian "Girka." The rather widely distributed variety "Yeoman I" was obtained by BIFFEN by crossing the white-headed Browick × Red Fife. The variety "Victor" was obtained by the English firm Gartons and Warrington by crossing in the following manner:

Squarehead × Red King
↓
Hybrid × Talavera
↓
Victor

Basically these are combinations of moist climate and steppe climate ecotypes.

One of the most productive of the west European varieties, Wilhelmina, was produced in *Holland* by the breeder BROEKEMA by crossing the varieties Spyk (Squarehead × Zealand White) × Squarehead. The cross was made in 1889; the variety was introduced into culture in Holland in 1901 whence it became distributed in other countries. The original squarehead variety came from England.

Swedish breeding has been principally based on the hybridization of English squareheads with local old northern Swedish varieties. The crossing of the latter with the highly productive West European types of soft wheat has been the outstanding feature of Swedish breeding.

German hybridization has been based on the use of local materials, with addition of squareheads from England and new breeding materials from Scandinavia. An important part in the formation of the German varieties was the use of *T. spelta*. This species has been particularly helpful in the development of varieties suitable for dry mountainous conditions with poor soil.

Argentine breeding has had very valuable results in combining Mediterranean steppe types of wheat with Chinese wheats. The noteworthy variety 38 MA (*i.e.*, No. 38 of the Ministry of Agriculture) was produced by the breeder BACKHOUSE by combining the Spanish variety Barleta with a typical non-shattering Chinese soft wheat having solid straw. The latter also conferred on 38 MA immunity from stripe rust. The Argentine breeder KLEIN made significant use of Japanese wheats through the Italian variety Ardito, obtained by crossing European soft wheats with a typical low-growing Japanese form.

* * * * *

From all the foregoing pedigrees of the world champion wheats, it can be clearly seen how the improvement of local varieties has been accomplished by using different ecological-geographical types such as Indian, Asiatic, West European, and Russian forms. In the creation of the spring forms of wheat in Canada and Alaska, an important part has been played by our northern wheats, such as those of eastern Siberia, which are distinguished by drought resistance during the first period of growth and early maturity, as in our North European forms. For improving winter wheat in America, particular value has attached to the use of our old steppe varieties, evidently borrowed from us in the distant past from the Trans-Caucasian region.

Thus actual world breeding practice discloses the necessity of having a wide geographic horizon in the selection of components for crossing. Ecological-physiological investigations of wheat give us a scientific basis for selecting parents. In this respect particular interest attaches to the recent studies of T. D. LISENKO on plant development by stages, with conscious selection of ecological types for obtaining forms suitable for definite, widely varied conditions.

T. D. LISENKO has shown that by selecting, for crossing, pairs of different ecological types, differing with respect to light in the "light stage" and to temperature in the first stage of growth, or naturally "vernalized," one might obtain, for given conditions of warmth and light, forms that are more cold-resistant and earlier than the original parents. Suppose, for example, that one parent is retarded in development in passing through the vernalization stage, while it passes through later stages rapidly, while another parent variety, on the other hand, is retarded in the blossoming stage, but passes rapidly through the vernalization stage under given field conditions. In crossing such parents one might obtain progeny which are earlier maturing, under these conditions, than the parental forms. Differences in behavior in growth stages, as shown by T. D. LISENKO, follow MENDEL's Law and can be classified. The method of a preliminary physiological grouping of forms according to their stage behavior may be used definitely and consciously in selecting parental pairs. Along this line there are most interesting possibilities in using extreme ecological types.

From the study of plant stages, as well as from the entire world experiments in breeding, it follows that it is not at all necessary to proceed on the principle of selecting the "best" forms to use as initial parents. From two "poor" wheats for given conditions, there may be obtained valuable forms. The breeder must know not only the laws governing the re-grouping of genes, but also the reactions of the original varieties to basic factors of development, considering the geographic origin of the parental forms. Physiological data must be related to the genetics of important physiologic characters.

Major ecological differences in wheat types ordinarily conform to the geographic distributions of the varieties.

The crossing of distantly related ecological-geographic types, as has been shown by world experiments and as theoretically follows from the nature of differences in stages of development in varieties, usually produces segregates which are earlier than the parents, and, with some combinations, forms that have a greater degree of cold resistance, and thus they give us the possibility of broadening the geographic limits of present-day wheat culture. In this way the culture of wheat has been extended in Canada, Australia, South Africa, and Sweden.

The individuality of varieties, their specific properties, has much significance in crossing. According to the experiments of E. F. PALMOVA, some types, such as the Japanese varieties, show a sharply expressed complex of dominance in segregation from crosses with European forms, in both the second and third generations. The Abyssinian types of hard wheat show a complex of dominance in crosses with other hard wheats. In the future, by means of cyclic crosses, it will be necessary to determine the role of the different components.

World experiments in hybridization of wheat have shown the great significance of complex crossing with the participation of several initial forms in the production of better bred varieties. A certain role is also played by backcrossing with the original parent forms. For bringing in certain characters,

for injecting into a good ecotype some character that is lacking, we need only add a few genes, not disturbing the general type. In this connection the method of back-crossing may have considerable importance.

Great possibilities for the selection of parents have been opened up recently by new knowledge of the composition of species and of species diversity. Breeding work of the past has been carried out primarily on soft wheats. The hard wheats have hardly been touched by the breeder. This is explained, largely, by the uniformity of the hard wheats. The hard wheats of western Siberia, Pri-Ural, the Don region, and the Lower Volga consist of rather uniform populations. We find a difference only in the Trans-Caucasian late hard wheats.

The extensive new materials that have been found within the limits of the groups of wheats with 28 chromosomes, permits a new approach to the selection of parental pairs in this group. There is particular interest to us, for improving our hard wheats in the immediate future, in use of the round-grained productive Syrian and Palestine race (type *horanicum*) which is distinguished by its early maturity, drought resistance, and resistance to lodging. As has been shown by experiments at the Institute of Plant Industry, this complex is dominant in hybridization with our ordinary hard wheats, as well as with other 28-chromosome wheats. Using the Syrian wheat as a basis, we may attempt to create a sort of Soviet "Marquis" among the hard wheats, including use of the awnless Abyssinian hard wheat. Theoretically this problem is entirely clear and definite: to secure earliness, drought resistance, and short straw from the Syrian wheat, awnlessness from the Abyssinian wheat, and to improve this combination with ecotypes of our hard wheat.

A most interesting assortment is seen in the productive hard wheats of North Africa which are highly resistant to rust and other diseases.

Considering the significant role of hard wheats in Russia, where they occupy approximately 4 million hectares, this problem appears to be a rather attractive one. In extending wheat ecotypes, the improvement of our hybrid wheats and their wider distribution is a problem of primary importance.

At the same time, in the group of 28-chromosome wheats there is a great diversity of ecological types which are sharply distinguished in their stages of development, which again reveals the great extent of possibilities in creating needed forms for different regions.

Crossing Closely Related Wheat Species:— Great practical interest attaches to the crossing of species with congruent genomes, characterized by the same number of chromosomes and producing fully fertile progeny. The discovery of a large number of new wheat species with valuable characters opens up new horizons. On the average, the seed set from crosses of wheat species of the same chromosome numbers, according to the forms used, varies from 20 to 60%. The F_1 is entirely fertile, and the reduction division is normal. The species (with the exception of *T. timopheevi* and *T. dicoccoides* within the 28-chromosome group) have homologous genomes. In the second generation there is the usual type of segregation with the great majority of the plants being entirely fertile *i.e.,* this proceeds just as in crosses of varieties within a single species.

Thompson and Robertson (1930) and Hollingshead (1932) have shown that the amount of irregularity in meiosis in the F_1 of interspecific wheat hybrids between parents of different chromosome numbers, varies, according to the species used, from 1.8 to 42%. Darlington (1931) has found that in hybrids of *T. turgidum* $\times$ *T. dicoccum* chiasmas are less common than

in the original parental forms, but on the whole this sort of hybrid produces fertile progeny, which is seen in the fact that irregularities in the behavior of chromosomes, in these cases, are comparatively small.

Within the limits of the 42-chromosome group of wheats, attention must be given to the use of the species *T. sphaerococcum* which has round, non-shattering grain and stiff straw, and to *T. vulgare compactum* which appears to have exceptional drought resistance and resistance to shattering. *T. spelta* also deserves attention. This species has minimum soil requirements and is comparatively winter resistant among our winter forms. In the same connection, attention should be given to the productive Afghan club wheats which have stiff straw, are non-shattering, and are rather cold-resistant, occurring in culture in Afghanistan at an altitude of 2800 meters.

There is particular practical interest for the breeder, in the immediate future, in the varied species and forms of 28-chromosome wheats, which have hardly been touched up to the present time. The discovery of new species with distinct contrasting physiological characters, such as *T. persicum,* the Abyssinian subspecies of *T. durum* and *T. turgidum,* and different ecological-geographical groups of emmers, creates the possibility of new combinations for different environmental conditions. The cold resistance of the spring-type high-mountainous *T. persicum* permits the extension of the culture of 28-chromosome or hard wheats to the northward. Experiments of the Institute of Plant Industry carried out in Detski Village (V. E. PISAREV) have disclosed interesting possibilities along this line. Preliminary work has shown that hybrids of the 2-grained *T. persicum* with hard wheats of different Abyssinian forms give very promising results in the North. The investigations of B. A. VAKAR and others have shown that in crossing *T. persicum* with *T. durum* the hybrids have well-balanced chromosome assortments, permitting the formation of normal pollen.

The Abyssinian hard wheats are valuable initial materials for improving our hard wheats by development of productive awnless forms. For increasing the yields of the 28-chromosome wheats, it is desirable to use the Mediterranean English wheats (*T. turgidum mediterraneum*) which carry in their genic complex a guarantee of highest productiveness under suitable conditions.

For the southern dry conditions, there is particular interest in the assortment of Syrian and Palestine hard wheats which have an ideal grain type, are suited to mechanical harvesting, and at the same time are distinguished by their drought resistance.

T. timopheevi has unique interest on account of its immunity from many diseases. According to the experiments of A. G. KHINCHUK (1929), in crosses with other species of the 28-chromosome group hybrids of *T. timopheevi* show considerable sterility, approximately ten times as much as in crosses of other 28-chromosome species of cultivated wheats among themselves. Sterility of the blossoms appears both in the F_1 and in later generations. This brings out the genetic peculiarity of the species. Nevertheless, *T. timopheevi* crosses more easily with the 28-chromosome group of wheats than with *T. monococcum,* which it resembles morphologically, physiologically, and ecologically. With the latter its hybrids are almost entire sterile in the F_1 generation (L. L. DEKAPRELEVICH and V. L. MENABDE, 1932).

The cytological investigations of *timopheevi* wheat of F. LILIENFELD and H. KIHARA (1934) in Japan, using cyclic crosses with different wheat species, *Aegilops,* and rye, have shown that in this species there is at least one unique genome (7 chromosomes) which does not conjugate with the chromosomes of species of the group of hard wheats (14 chromosomes) nor with those of rye,

Aegilops, or einkorn. This fact has particular importance, showing that in *T. timopheevi* there is a distinct assortment of 7 chromosomes which is different from those of other wheat species, thus supplementing the three groups (3×7) of soft wheats. It is possible to incorporate into the genus *Eutriticum* a fourth assortment specific for *T. timopheevi*. Crossing *timopheevi* wheat with other species which are characterized by having 14 chromosomes (haploid number) despite the similarity in chromosome numbers, reveals the genetic peculiarity of this species.[75]

Crosses of Species with Different Chromosome Numbers:—RIMPAU, so far as we know, was the first to cross wheat species of different chromosome numbers, and even to attempt to determine, according to Mendelian principles, the relationships in segregation. Extensive practical work on the use of hybridization of wheat species with different chromosome numbers began toward the end of the 19th century and is associated with the names of VILMORIN in France and FARRER in Australia.

Despite the great success in the practical use of crosses between different geographic races within a single species or closely related species, the use of crosses between wheats with different chromosome numbers until recently has met with considerable difficulty. Hybrids between hard and soft wheats have been obtained on a number of occasions, beginning with the '80's of the past century, but these have not become widely distributed, although they have continually attracted the attention of breeders. An interesting form of awnless hard wheat obtained by crossing ordinary hard wheat with awnless soft wheat was obtained in Australia under the name "Hugenot." However, despite the considerable time that has elapsed since its production, it has not become widely distributed, although it has been repeatedly tested in the field in many regions, particularly in Tunis, Algeria, and Morocco. In Australia this hybrid is used principally for green forage.

An important work on the hybridization of hard and soft wheats has been carried out in Tunis by the well-known breeder, BOEUF. He somewhat improved the Australian hybrids by crosses with Tunisian hard wheats, but his hybrids did not extend beyond the limits of the experiment stations. The most interesting practical result in crossing wheats of different chromosome numbers was obtained by MCFADDEN in South Dakota, as a result of crossing a Russian emmer with the soft wheat "Marquis." From it, in the sixth generation, he obtained the hybrid varieties "Hope" and "H-44." These varieties have interest for their resistance both to leaf rust and to loose and covered smut.

HAYES, KURTZWEIL, and PARKER obtained hybrids by crossing hard wheats with "Marquis." The variety "Marquillo," obtained in this way, has 42 chromosomes, just as common wheat, and today is widely grown. Finally there has been obtained a valuable hybrid by crossing "Marquis" with a hard wheat named "Pentad," which had been brought by Professor BOLLEY from Russia. This hybrid is also distinguished by its awnlessness and its resistance to rust. In any case the number of valuable hybrid varieties obtained by crossing wheats of different chromosome numbers is still very limited and easily appraised.

The most valuable results in hybridizing hard and soft wheats obtained by us in SSSR have been principally at the Saratov Station, as a result of 15 years of persistent work. This has produced the varieties "Sarrubra," "Sarroza," and "Blansar." The particularly valuable variety "Sarrubra" today is being widely grown and evidently has an important future. As early as 1934

[75] H. KIHARA: Genomanalyse bei *Triticum* und *Aegilops*. F. LILIENFELD and H. KIHARA: *Triticum timopheevi* Zhuk. *Cytologia* 6 (1): 87-122, 1934.

the area planted in this variety, according to the estimates of G. K. MEISTER, was approximately 200,000 hectares, and by 1937 it had increased to 1,400,000. This variety is noteworthy for its non-shattering, awnlessness, and excellent grain. On the other hand, it requires further improvement by crossing, as indicated by its susceptibility to smut.

Analogous hybrids have been obtained by Professor P. N. KONSTANTINOV, but these are not yet widely distributed, nor are hybrids produced by the Odessa Station.

Evidently the emmers (*T. dicoccum*) deserve more attention in crossing with soft wheats, as is seen from German work as well as that of the Kharkov and Shatilov Stations.

The Shatilov and Kharkov Stations have carried out extensive experiments on the hybridization of emmers with soft wheat. A number of interesting forms have been produced, but these varieties still have not attained commercial status.

The experiments of the Saratov Station have shown that it makes a difference which of the species serves as maternal parent. If the maternal parent is soft wheat, the success in crossing is lower, but the percent of viable seed is higher. If the maternal form is hard wheat, the fertility is greater, but the seed produce fewer seedlings. In practice the latter combination is most useful. This conclusion has been confirmed by the cytologists WATKINS (1927) and THOMPSON and CAMERON (1928 and 1930). They have shown that in crosses between 21-chromosome and 14-chromosome species of wheat, plump grains are formed when the maternal parent is the 21-chromosome variety and shrivelled grains when this is the paternal parent. Such differences in grain development are due to the fact that the maternal plant supplies two nuclei for the formation of endosperm, while the male parent only supplies one, as has been shown by SAX (1921).

The same thing has been observed in crosses of *T. dicoccum* (14 chromosomes) with *T. monococcum* (7 chromosomes). Normally germinating seed are formed in those cases in which *T. dicoccum* is used as the maternal form, but not in the reverse case (THOMPSON, 1930; WAKAKUWA, 1930).

OEHLER (1934), as well as WAKAKUWA (1934), has considered that the crossing of wheat species of different chromosome numbers proceeds more easily when the species with the smaller number of chromosomes is chosen for the maternal parent, but the viability of seed is greater when the paternal parent has the lesser number of chromosomes.

In the following table are given data from the Saratov Station (1934) comparing the yields and quality of parental varieties and of the hybrids obtained from them.

Yield of Grain and Milling-Baking Quality of Spring Wheat Varieties:—

Name of Variety	Yield of grain in tsentners/ha. 1933	Yield of grain in tsentners/ha. Av. 9 yrs., 1925-1933	Milling-baking quality, av. for 4 yrs. (1929-1932)		
			Yield of flour in percent	Volume of loaf	Baking value
Sarroza	8.6	14.9	78.2	562	87
Sarrubra	8.2	14.7	78.4	571	90
Blansar	8.0	14.4	77.9	536	89
v. *lutescens* pure line 062	8.4	15.5	75.0	496	79
v. *hordeiforme* pure line 0432	4.5	11.1	75.0	523	85

From the data presented it is seen that the hybrid varieties surpassed the hard wheat parent in quality and yielded approximately as much grain as the soft wheat parent. In addition the hybrids were distinguished by excellent appearance of grain and non-shattering.

Genetic investigations of crosses of species with different chromosome numbers have disclosed certain regularities in the behavior of hybrids and in the process of their formation. On the average, the percent of seed set from crossing 14- with 21-chromosome wheats varies from 10 to 30% (OEHLER). The F_1 often has sterile blossoms. In the second generation in such crosses there is observed a great diversity of form with many new types, much disharmony, and many plants with a greater or less degree of sterility or even complete sterility. Characteristic for this group of crosses is a broad diapason of variations in segregation. In the hybrid progenies there appear certain characters which are peculiar to other species of wheat, including the brittleness of rachis of wild forms (*T. diococcoides*). The great majority of plants of the second generation usually are disharmonious, abnormal, with more or less sterility. In crosses of *T. dicoccum* × *T. vulgare, T. vulgare* × *T. turgidum,* and *T. vulgare* × *T. persicum,* there appear new forms which are distinct from the parental plants, for example, forms with inflated glumes, forms with awnlike processes on the glumes, the squarehead type, loose- and compact-headed forms, and speltoid forms. Variation is particularly wide in the form of the glumes. There appear forms with delicate, thin awns and on the contrary, coarse-awned types (*rigidum*); in many combinations there are found forms with narrow, almost awl-like leaves, albinos, and semi-albinos. At the same time, in different combinations of crosses of species with different chromosome numbers (21 × 14), on the whole there is repeated the same range of new forms.

The occurrence of such uniformity in variation points to a common cause, and induces us to look for a general scheme in the course of hybrid variation.

At the same time, in all these variations (we are speaking here of crosses of 14-chromosome with 21-chromosome species) there appear definite improved types, the number of which clearly increases in the third generation. It is noteworthy that some of the segregants remain constant from the time of their first appearance.

A. A. and L. A. SAPEHIN (Odessa Institute of Genetics and Breeding) have shown that in the F_2 and F_3 in segregation there appear valuable gene complexes which become stabilized into constant types. For arriving at practical results in production of valuable combinations from hybridizing hard and soft wheats, the work must be carried out on a large scale (in Odessa from 1.5 to 2 million plants in the second and third generation). It is characteristic, in such crosses, for there to appear lethal factors in many combinations, with a high degree of pollen sterility in many plants of the F_2. This is particularly the case in crosses of einkorns with hard wheats and even more so when einkorns are crossed with soft wheats. In the first case, in the second generation there appears a very limited assortment of forms (N. VAVILOV and O. YAKUSHKINA, 1925), but it is noteworthy that these few forms, even in the second generation, are constant and contain combinations of characters of both original parents. Unfortunately the majority of these forms have little practical value because of their low productivity.

L. A. and A. A. SAPEHIN, who made a careful cytological and genetic study of hybrids of hard and soft wheats, observed the possibility of obtaining definite complexes of the genes of the two parents with chromosome numbers similar to that of one of the parental forms.

In all cases, in crossing species of different chromosome numbers, great importance attaches to the particular varieties of parents chosen. The behavior of different varieties is dissimilar in such crosses, particularly from the standpoint of fertility. Some of the combinations show comparatively normal seed

production. In this connection there is particular value in the use of cyclic crosses involving a large number of components. The use of crosses of species of different chromosome numbers to obtain in a short time useful results, requires very extensive work, considering that the overwhelming majority of forms which appear in the first filial generations have little value, being non-productive or even sterile.

In the past decade there have been a number of cytological investigations of hybrids from wheats with different chromosome numbers, showing to a considerable extent the causes of disharmony, sterility, and impracticability of certain combinations (KIHARA, SAX, WATKINS, THOMPSON, BLEIER, L. A. and A. A. SAPEHIN, and others). There is a résumé of data on the cytology of wheat hybrids in the book edited by B. A. VAKAR (1934).[76]

The cytology of hybrids of species with different chromosome numbers has been studied to a considerable extent in wheats and in particular in the pentaploid hybrids obtained from crossing 21- and 14-chromosome species ($2n = 35$). These hybrids in meiosis are characterized by a high degree of irregularity, differing in this respect from hybrid wheats obtained from parents with the same chromosome number. Disharmonies in such crosses, as the cytological investigations have shown, are associated with an incompatibility of chromosomes in crossing. Not all the chromosomes find corresponding homologous ones for pairing, and there result univalent chromosomes, the greater or lesser number of which determines greater or lesser anomalies in development and sterility. Sterility is associated with processes occurring in the reduction division. The genomes of einkorn (A), a number of species of hard wheats (AB), and soft wheats (ABC), each of which consists of an assortment of 7 chromosomes, do not meet with fully homologous assortments of chromosomes in crossing, as a result of which, whole assortments may remain univalent. The genome of hard wheats ($AB = 7 + 7$) is homologous with part of the genome of soft wheats ($ABC = 7 + 7 + 7$), and the 14 chromosomes of hard wheats resemble those of soft wheats, and form bivalents with the latter. Seven of the chromosomes of soft wheat do not find corresponding partners, and remain univalent and distributed at random. The gametes formed contain 14 to 21 chromosomes. The plants of the second generation are characterized by a corresponding 28-42 chromosomes. Simple Mendelian segregation, therefore, does not occur in this case. As a result of this disharmony there survive, in segregation, principally those progeny which have increased the number of their chromosomes up to 42 or those which have reduced them to 28. In the group of plants of the F_2 with chromosome numbers from 28 to 34, in later generations there is observed an increase in the number with 28 chromosomes; in the group of plants of the F_2 with chromosome numbers from 35 to 42, the reverse process occurs, tending toward plants with 42 chromosomes. The whole mass of hybrids with intermediate chromosome numbers, approximately 35 (2n), are eliminated, since they ordinarily have little possibility for survival.

KIHARA, SAX, THOMPSON, L. A. and A. A. SAPEHIN, and others have carefully studied the cytological picture related to the behavior of different types of plant hybrids. The majority of plants in the second and third generations of hybrids between hard and soft wheats usually produce forms with a considerable number of univalent chromosomes. At the same time there are produced plants with chromosome numbers similar to those of the parents. These latter ordinarily resemble the parents in appearance, although they con-

[76] [Materials for the study of wheat hybrids. Cytological symposium.] Siberian Institute of Grain Husbandry, Omsk, 1934.

tain certain genes of the other parent. A. A. SAPEHIN has demonstrated the rare occurrence of balanced types of wheat with 36 chromosomes.

The great majority of combinations with intermediate numbers of chromosomes (possibly excluding the 36-chromosome wheats of SAPEHIN) do not survive, while gametes with chromosome numbers 14 and 21 are more viable. The investigations of VAKAR and his co-workers (1934) have shown that cytological processes in morphologically-constant, awnless hybrids of *T. durum* and *T. vulgare,* even in the 7th generation, are still insufficiently stabilized, which probably explains the difficulty experienced in breeding work throughout the world in attempting to attain fully productive hybrids of *T. vulgare* × *T. durum.*

Only work carried out on an extensive scale and continued through many generations leads to positive results.

Hybrids with 42 chromosomes, according to external morphological appearance, belong to the *T. vulgare* group, while those with 28 chromosomes belong to the *T. durum* group. Biological characters display the same tendency, although there is a possible exception in which hybrids having the external appearance of *T. vulgare* may possess biological characters, for example, immunity from rust, inherited from *T. durum.*

It is practically very important that when the work is conducted on a broad scale there may be rarely obtained from such crosses, forms which combine the valuable properties of the parents and have a balanced genome and characters inherited from both species, *i.e.,* it is possible to obtain a hard wheat with certain valuable characters of soft wheat, or the reverse. From the group of 28 chromosomes, in this way, the possibility has been revealed, when working on an extensive scale, of combining in a soft wheat such valuable characters as early maturity, drought resistance, resistance to diseases, and a good quality of grain.

Disharmonies in the behavior of chromosomes do not appear to be limited to hybrids between wheats of different chromosome numbers. SAPEHIN also found chromosomal disharmonies in crosses of different geographic groups belonging to a single wheat species and also cytological disharmonies within the limits of certain pure lines. Also L. A. SAPEHIN has shown that there are special genes which disorganize the normal reduction division, disorganizing genes, as well as genes governing the formation of cross walls, diads, and tetrads, the action of which may cause the formation of diploid gametes (giant pollen grains). L. L. DEKAPRELEVICH has shown that, in some cases, there appear sterile hybrids as a result of crossing varieties of a single wheat species. These facts must be kept in mind, but they concern comparatively rare cases, with hybrids between species of different chromosome numbers usually having the behavior described above.

In the preceding chapter this phenomenon was noticed in crosses of *T. timopheevi* (haploid number 14 chromosomes) with hard wheats and emmers having the same number of chromosomes. One of the genomes of *timopheevi* wheat is not homologous with any genome of hard and soft wheats.

As for *einkorns,* as we have seen, these are difficult to cross with either 28- or 42-chromosome wheats. The percent of viable seed obtained from such crosses in combination with 42-chromosome species is not greater than 1-2%, and in crosses with 28-chromosome species einkorns usually produce no more than 10% seed (OEHLER).

The F_1 is commonly sterile; the pollen lacks protoplasm. Only one genome (A) of hard and soft wheat is homologous with the genome of einkorn.

Backcrossing the F_1 with the parents is difficult.

Sterility in hybrids of species with different chromosome numbers is usually associated with sterility of the pollen. In the embryo sac, evidently, there are most frequently present normal female gametes which do not undergo reduction division, giving them a number of chromosomes which is close to the diploid number.

The use of hybrids of soft wheats with einkorns is more difficult than with hard and other species of the 28-chromosome series, particularly because of the exceptional sterility of the F_1 and the difficulty of backcrossing, but theoretically the possibility is not excluded that in some cases, although they may be rare, there can be obtained interesting combinations. BLARINGHEM in France obtained a fertile hybrid of einkorn with hard wheat. This hybrid at one time attracted attention because of its immunity from rust, but it had little productivity and today it is entirely lacking from the list of French varieties. We obtained the same sort of hybrid in crossing einkorn with *T. persicum* (1925). With very distinct species, such as we have in crossing 28- and 14-chromosome wheats, in the F_2 and F_3 there are very few successful combinations, but, as we have shown (1925), these tend to be constant even in the F_2 and F_3. Practically, hybrids such as these have not given the results that were anticipated by some investigators (BIFFEN).

According to the investigations of L. L. DEKAPRELEVICH and V. L. MENABDE, hybrids of *T. monococcum* with *T. timopheevi* (even from a single region of cultivation in western Georgia) gave sterile plants in the F_1 (not a single seed from 300 heads).

The complex type of segregation observed in crossing 28- and 42-chromosome wheats, which results in great diversity, new formations, and sterility, we have named (1925) in honor of the French investigator NAUDIN who, before MENDEL, described such phenomena as usually occurring in crosses of species of different chromosome numbers giving more or less fertile progeny.

Wheat-Rye Hybrids:— Experiments in the crossing of rye with wheat were made on more than one occasion in the 19th century without any important results for breeding. A new era in this work has begun in the Saratov Station.

In 1917 in Saratov there occurred a massive natural hybridization of soft wheat with rye. The blossoming times of wheat and rye coincided during this year, resulting in a great number of natural hybrids. We might say that nature itself carried out a vast experiment in hybridization. If this experiment were to be repeated using ordinary means of artificial hybridization, it would require a whole army of breeders. We know of no other analogous experiment in world practice on the same scale as that which occurred at the Saratov Station. In 1918 there were collected 300 hybrid seeds of wheat and rye, a number heretofore unknown in history; a particularly large number of hybrids were obtained from the pure line of wheat 0648. The experiments of BACKHOUSE in Argentina and the work at the Saratov Station showed the important role of the individuality of the wheat variety in crossing with rye. Thus in BACKHOUSE's experiments one Chinese wheat gave a percentage of seed set from pollination with rye that was almost the same as would result from pollination with the same species of wheat. In the experiments of G. K. MEISTER, at the same time at which the pure line of wheat 0648 gave 61% successful crossing, another pure line 0329 gave only 3.6%. The Central Asiatic soft wheats crossed with rye with particular ease (V. N. LEBEDEV).

Natural hybrids of wheat and rye have been found during the past decade in Ukraine (V. N. LEBEDEV), by us in Iran, and by LEIGHTY and HOOVER in USA, as well as at Saratov. It is evidently more easy to cross rye with soft

wheats, but it is possible to do it with hard wheats. L. N. DELONE and FRANKEL, out of 15,000 pollinated blossoms of hard wheat, obtained 0.15% seed. Emmer (*T. dicoccum*) has also been successfully crossed with rye (G. K. MEISTER). As shown by B. I. VASILEV, 1932, the seed of hybrids of hard wheat with rye usually are not viable.

The pollination of rye by wheat, although it can be accomplished, is much less successful, which in part is due to technical difficulties. Hybrids of this sort are indistinguishable from wheat-rye hybrids (A. BUCHINGER, 1931, G. K. MEISTER).

A summary of the work at the Saratov Station on the hybridization of wheat with rye, as well as historical data on this question, are given in the book "Rye-Wheat Hybrids" by G. K. and N. G. MEISTER (1924).

The first generation of hybrids of soft wheat with rye are self-sterile as a result of failure of pollen to develop, failure of the anthers to open, or other causes.

Wheat-rye hybrids behave like hybrids of other distant crosses with different numbers of chromosomes in the parents, and a lack of similarity of the chromosomes; *the chromosomes of wheat and rye do not conjugate;* the first generation is usually sterile as a result of anomalies in the reduction division.

The female gametes evidently are more viable: pollination of the first generation with wheat or rye pollen may produce a limited number of seed.

With repeated backcrossing of the F_1 hybrids with wheat, fertilization is easier than in repeated backcrossing of the F_1 with rye.

Seed usually do not result from self-pollination of the F_1; even in the rare cases where this does succeed, seedlings do not result because of non-development of the embryo.

Plants of the F_2 obtained by backcrossing with wheat usually contain more than 42 chromosomes. Ordinarily in the F_2, and particularly in later generations, there appears a tendency to approach the wheat type with 42 chromosomes, which is associated with an increase in fertility of the hybrids.

In the second generation (from backcrossing with wheat) there is marked segregation, according to the data of the Saratov Station, and there have been observed to be about 35% entirely non-fertile plants; in certain years this number increases to 62%, but at the same time among these hybrids there are some plants which approach the wheat type and have complete fertility.

The process of development of forms is quite singular.

The great extent of the work at the Saratov Station and the large number of hybrids first made available to investigators, disclosed a number of important facts. Just as in crossing wheat species of different chromosome numbers, in the progeny of the rye-wheat hybrids there were observed many new types: white-grained forms where the parents had red grains; the appearance of characters ordinarily found only in rare varieties; squareheaded types characteristic of the improved varieties of western Europe; inflated glumes ordinarily found in forms of soft wheat of southwestern Asia; coarse heads (*rigidum*); speltiform type of glumes; loose and compact plants; and finally, forms very much like *T. dicoccum.* Some of the hybrids resembled hard wheats. There were obtained forms of wheat with hairiness under the heads—a character which is very rare in wheat, but common in rye. In some forms there was observed the brittleness of heads of *T. dicoccoides, i.e.,* there occurred the phenomenon noted by LOVE and CRAIG (1919) in crossing *T. vulgare* × *T. durum.*

A noteworthy shifting about of characters in soft wheat types occurred with respect to physiological properties. Whereas the original form of soft wheat 0648 (type of the variety "Cooperatorka") is distinguished by a low degree

of winter resistance, among the plants of wheat type in the hybrid progeny there appeared forms with much more winter resistance, which demonstrates the role of rye in increasing cold resistance in the hybrids. The investigations of the Saratov Station definitely showed the possibility of increasing the cold resistance of wheat by crossing with rye, although this did not reach the degree of resistance found in rye. A number of the hybrid forms of the wheat type were interesting from the standpoint of milling-baking quality. There occurred the form 46/131 which, in yield and cold resistance, was approximately the same as the best Soviet cold-resistant standard variety—0329 (produced by the Saratov Station). Recently there has been found the hybrid 434/154 which equals and sometimes surpasses 0329 in cold resistance.

In the opinion of G. K. Meister, in such crosses there occur not only segregation, but also mutation processes. Very rarely in the progeny of the hybrids there are found plants resembling the rye type (a few individuals in many thousands of plants). In general, in segregation there is a tendency toward the type of the wheat parent.

Intermediate types, which are found in large numbers, are either sterile or only weakly fertile. The great majority of plants are of the wheat type with some of them sterile but many with normal fertility.

There have been found amphidiploid forms with 56 chromosomes (rye has 14 chromosomes, the wheat parent 42 chromosomes). More than 20 plants of intermediate types, found in the second generation among a large number of plants in 1926-1927, showed almost normal fertility and non-segregation in later generations. According to the investigations of G. A. Levitski they were typical amphidiploids with 56 chromosomes (42 chromosomes of wheat and 14 of rye). These amphidiploids, which combined characters of rye and wheat, were called by G. K. Meister *Secalotricum*. Oehler has called these forms *Triticale*. The same types of amphidiploid forms were found in considerable number by V. N. Lebedev (1934). In cold resistance they are inferior to the standard winter wheat 0329 and their milling and baking quality is considerably lower than that of wheat. In crosses with rye, *Secalotricum* gives from 30 to 50% successful fertilization, but the grain obtained usually does not germinate. In crosses with wheat, the percentage of fertilization is much higher and the grain germinates almost normally. In such hybrids the first generation has nearly normal fertility, and in later segregations there appear wheat-like forms although they are quite variable, evidently because of the presence of the rye chromosomes.

The use of amphidiploids in future hybridization work may very possibly aid in solving a number of practical breeding problems.

The cytological picture of the behavior of rye-wheat hybrids (not amphidiploids) has been studied by Kihara (1919) and also by V. R. Zalenski, A. V. Doroshenko, Bleier, W. Thompson (1926), V. N. Lebedev (1932, 1933), and G. Kattermann (1934), who have found much disharmony, with unbalanced chromosome apparatus and univalent chromosomes. The genome of rye (7 chromosomes) is not homologous with any of the genomes of wheat species (ABC) and bivalents in the F_1, due to a combination of rye and wheat chromosomes, are formed to very small extent (V. N. Lebedev). If such do appear in limited numbers, the possibility is not excluded that this may be due to autosyndesis of chromosomes of the soft wheats (V. N. Lebedev, 1932, 1933). Moreover it is characteristic for the union of chromosomes, if this does occur, for this to be as rings, and not lengthwise as is customary in crosses between closely related parents.

The number of chromosomes in plants of the F_2 obtained by backcrossing

the F_1 with wheat, usually varies between 38 and 49. The majority of plants have 47-49 chromosomes, 42 of wheat + 5-7 of rye. These latter are eliminated in later generations, and in the F_3 and F_4 most of the plants are characterized by having wheat chromosomes and an external appearance resembling wheat. These wheat-like plants are entirely fertile and their reduction division proceeds normally. Another fraction of the progeny which still retains rye chromosomes (and rye characteristics) is distinguished by its high sterility and irregular reduction division. However, rarely among these plants there appear completely fertile forms with rye characters, which is evidently explained by their having a full assortment of rye chromosomes in place of wheat chromosomes or an interchange of part of the rye chromosomes. A number of such fully fertile new types are known. V. N. LEBEDEV (1932, 1933) in Ukraine has obtained, by repeated hybridization, an F_1 and also F_2 with a balanced set of 28 rye chromosomes. These forms contain a somatic assortment of 14 rye chromosomes and 14 wheat chromosomes, *i.e.*, in this case there has been autosyndesis of wheat chromosomes.

In one hybrid seed V. N. LEBEDEV found a high degree of autosyndesis. In the pentaploid plants in the F_2 generation from this seed, having one assortment of chromosomes of soft wheat and two homologous assortments of rye, in meiosis there were found 12-14 bivalents; seven of them evidently were formed by conjugation with rye homologs, and seven others from autosyndesis of bivalents among the soft wheat chromosomes from its haploid assortment, *i.e.*, there was conjugation of two of the wheat genomes while the third remained in univalent condition. The reduction division in this 28-chromosome form was comparatively normal and 70% of the pollen was well-developed. The fertility was about 60%. Morphologically this form was distinct from both wheat and rye. The progeny of this form, while retaining its chromosome composition, appeared to segregate with respect to characters of a racial sort, retaining the general morphological type.

Apparently certain forms of wheat have a tendency to autosyndesis in crossing with rye (V. N. LEBEDEV).

The Saratov Station also observed hybrids with 28-29 chromosomes that were quite cold-resistant but did not mill satisfactorily.

There is great practical interest in hybrid progenies in the group of plants of the wheat type to which the Saratov breeders have been giving concentrated attention.

The significant diversity of this group, extending beyond the limits of the wheat parent, leads us to consider it possible to obtain desired combinations with the quality of wheat and the cold-resistance of rye. Many of the new forms are not very distinct from wheat, *T. vulgare*. Some of these are typical soft wheats, but there are found, as has been shown above, other forms which have definitely borrowed morphological characters on a 42-chromosome basis. Further investigation of the rye-wheat hybrids has particular interest, and in any case we know that there is a theoretical possibility of transferring properties of rye to wheat. The regrouping of chromosomes, including autosyndesis and the possibility of obtaining a multitude of diverse amphidiploids (V. N. LEBEDEV), opens up new possibilities, which we did not know of earlier, in the sense of obtaining fertile balanced forms. The combining of characters of rye and wheat has also great interest from the standpoint of transferring from rye to wheat winter resistance, disease resistance, early maturity, and tolerance of poor soil conditions. The German breeders are particularly interested in creating wheat varieties for light soils.

We must definitely point out, however, that to obtain combinations of the

most valuable wheat characters with the winter-resistance of rye and its low soil requirement is a difficult problem. Despite the great amount of work done in Saratov during the past 18 years, the workers there (G. K. MEISTER) recognize that they are still far from a practical solution of the ideal combination of the winter-resistance of rye with the high quality of wheat. In the experiments of the State variety tests, the best rye-wheat hybrids yet obtained, 46/131 and 21/36, have not shown notable advantages over ordinary varieties of soft wheat, either from the standpoint of winter-resistance or from that of quality. While they somewhat surpass the parental forms in winter-resistance, they still are inferior to rye in this respect. It is possible that in this connection a more interesting wheat-rye hybrid variety is *erythrospermum* 12/15 of the Saratov Station, at present being increased, which has good baking qualities, surpasses *hostianum* 0237 in cold-resistance, and at present appears to be the most reliable winter wheat in the steppe region of Ukraine and the northern parts of North Caucasus. "Meanwhile," writes Professor MEISTER[77] (1934), "we have not succeeded, with wheat-rye crosses, in jarring soft wheat away from dead center with respect to the property of cold-resistance. The question is much more complicated than it appeared to be in the beginning of the investigation" (p. 69).

Amphidiploids which are encountered among the hybrids of rye and wheat, in later generations are represented by original forms which combine the qualities of rye and wheat with comparatively normal productivity, but unfortunately they do not come up to the requirements set by breeders. They could be used for further crossing.

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Extensive work on rye-wheat hybrids during the past ten years has been carried out in the Argentine station directed by Dr. WILLIAMSON with whom we became acquainted in 1933.

In contrast to the Saratov work, the attention of the Argentine breeders has been mainly directed toward intermediate types from the standpoint of head morphology and lodging, and in this respect they have obtained desired combinations. As a result of persistent work the Argentine station has obtained fully productive forms which in external appearance are intermediate between wheat and rye. These unusual plants belong systematically neither to wheat nor to rye. According to the investigations of D. KOSTOV (1934) these hybrids have 42 chromosomes as in soft wheats. In quality of grain, difficulty in milling, and low yields as compared with wheat, these plants cannot compete with wheat. The Argentine station is carrying out very extensive work in backcrossing, but still these forms do not rival wheat.

In any case, the extensive work over many years of the Saratov and Argentine stations shows the difficulties with which the practical breeder must contend in working with intergeneric hybridization of wheat and rye, and which we must consider in proceeding with this type of cross. This work must be pursued on a broad scale, with great persistence and cytological control. It is possible that the working out of new methods, wider use of backcrossing, and the selection of new biotypes or other species may bring us to a more speedy solution of this practical problem.

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A. I. DERZHAVIN has worked on a broad scale crossing wheat species with *Secale montanum*—perennial rye, and obtained a large quantity of hybrid seed

[77] G. K. MEISTER: [Summary of work of the Saratov Breeding Station on Interspecific and Intergeneric Wheat Hybridization]. Sbornik Sel.-Kh. Nauka v SSSR. Vaskhnil 1934.

(up to 200,000). On self-pollination the F_1 is usually sterile. In crossing with wheat there were obtained 164 grains from 189,474 blossoms, *i.e.*, 0.09% successful pollination. The most difficult was crossing perennial rye with einkorn and *T. dicoccum*. The perennial form of life of rye, and the brittleness of its rachis were dominant. In later generations A. I. DERZHAVIN was able to obtain wheat with a perennial form of life. The practical value of this is obvious.

Wheat-Aegilops Hybrids:— Systematically, the genus *Aegilops* has been worked over very thoroughly in the recent investigations of P. M. ZHUKOVSKI and A. G. EIG of Palestine and on the cytological side by SENYANINOVA-KORCHAGINA. *Aegilops* is very rich in species and varieties. The history of hybridization of wheat with species of *Aegilops* embraces an entire century. In 1826 FABRE described natural hybrids between wheat and *Aegilops* under the name *A. triticoides*. On finding these intermediate forms, the nature of which was unknown, botanists of the 19th century were inclined to regard them as an ancestral form of wheat, indicating an evolutionary series from *Aegilops* to the cultivated wheat species of the present. The careful work of GODRON (1854-1877) however, showed very clearly the hybrid nature of these intermediate plants and the role, in their formation, of backcrosses with the parental forms.

Almost all leading botanists of the middle 1900's became interested in the wheat-*Aegilops* hybrids. EDWARD REGEL, Director of the St. Petersburg Botanical Garden, at the same time as GODRON, disclosed the hybrid nature of *A. triticoides*.

With the explanation of the role of hybridization in the formation of intermediate forms, interest in this question lapsed and there began a period of inertia which was broken by renewed interest in *Aegilops*-wheat hybrids in the 20th century, in connection with discoveries in the field of cytogenetics. In nature there was discovered a massive occurrence of hybridization of *Aegilops* with wheat. PERCIVAL in 1924 suggested the participation of certain *Aegilops* species in the origin of *T. vulgare*. On the basis of the homology of 7 chromosomes of *Aegilops cylindrica* with chromosomes of soft wheat (genome C), giving 7 bivalents in crosses with *T. vulgare,* and the combining of the chromosomes lengthwise and not in ring formation as is usual in distant crosses, for example in rye with wheat, and also on the basis of morphological similarities of the heads of this species with *T. spelta,* PERCIVAL proposed that the origin of wheat was by natural hybridization of wheat of the emmer group with some species of the genus *Aegilops*. SAX, on the basis of cytological investigations, did not share the hypothesis of PERCIVAL.

There began extensive experimental work in crossing species of *Aegilops* with different species of wheat. Recently this work has occupied dozens of investigators.

All species of *Aegilops* will cross with different wheat species, particularly when *Aegilops* is used as the maternal parent. The average percent of successful pollination in such crosses, according to OEHLER, is 6.8%. The species which blossom at the same time cross most easily. The number of chromosomes in the species used, according to the investigations of OEHLER, does not have great significance; species with 7 chromosomes appear to cross least readily with wheat species, but this question still needs experimental verification, considering the great number of species of *Aegilops*.

Usually the seed from such crosses germinate well, but when the crosses are accomplished with difficulty, germination is poor.

The F_1 has intermediate characters, but in general the *Aegilops* type is clearly dominant. This is specific for all crosses of wheat with this genus. Plants of the F_1 are usually sterile, and the anthers do not open. With self-pollination, seeds, as a rule, are not obtained. Backcrossing with the parents gives poor results (0.3-0.4%). If the plants are cross-pollinated among themselves, there is obtained on the average one seed per 312 blossoms, according to OEHLER's calculation.

The sterility is explained by disharmony in the reduction division, the chromosomes of species of wheat and *Aegilops* being non-homologous, or only partly homologous. Up to this time, only in the species *Aegilops cylindrica* has been found one genome (C) which is fully homologous with the genome C in soft wheat. All other genomes of *Aegilops* species (D, E, F, G, and S) are not homologous with chromosomes of cultivated wheat or only partly so (OEHLER). As a rule there is observed either a majority of univalents or a joining of wheat and *Aegilops* chromosomes in ring fashion and not lengthwise: this indicates that *Aegilops* is quite distinct from wheat.

As shown by cytological study of hybrids of *Triticum* × *Aegilops*, there are frequent cases of non-reduced gametes, which is associated with partial univalence of the chromosomes. This makes possible the occurrence of amphidiploids, having intermediate characters, and at the same time constancy and fertility (*Aegilotricum*). There is a particularly large number of cases of amphidiploids in hybrids between different 28-chromosome species of wheat and different species of *Aegilops*. Such amphidiploids were obtained by CHERMAK in crossing *A. ovata* × *T. dicoccoides* (n = 28), BLEIER (1926) by crossing *A. ovata* × *T. durum* (n = 28), KIHARA and KATAYAMA (1931)—*T. dicoccoides* var. *kotschianum* × *A. ovata* (n = 28), PERCIVAL—*A. ovata* × *T. turgidum* (n = 28), BLARINGHEM (1931)—*A. ventricosa* × *T. turgidum*, and KIHARA and KATAYAMA—*A. cylindrica* (n = 14) × *T. vulgare*.

A number of amphidiploids were also obtained by O. N. SOROKINA in the Institute of Plant Industry, namely *A. longissima* (2 n = 14) × *T. durum*, *A. triuncialis* (2 n = 14) × *T. dicoccoides*, *A. triuncialis* × *T. dicoccum*, and *A. triuncialis* × *T. polonicum*. These amphidiploids are distinguished by almost normal fertility, normal conjugation of chromosomes, and a combining of the genomes of wheat and of species of *Aegilops*. The plants are self-fertile. They might quite logically be considered as new species. The amphidiploids have been used for genetic study and there have been obtained new forms with still greater numbers of chromosomes. Although they have great theoretical interest respecting the problem of species formation, the amphidiploids obtained, despite their fertility, unfortunately are far from the forms which breeders need, since they have inherited from *Aegilops* a number of undesirable characters, such as small grain, persistant retention of the grain within the glumes, and brittleness of the rachis.

Great interest attaches to forms which do not have a complete assortment of the parental chromosomes, but which have a balanced chromosome complex with almost normal productivity of the plants, and at the same time combinations of characters of wheat and *Aegilops*. Such forms have been obtained by O. N. SOROKINA in crossing *A. triuncialis* × *T. dicoccum*, *A. triuncialis* × *T. dicoccoides*, and *A. ovata* × *T. persicum*. In the latter case there was observed a well-marked segregation in later generations for a number of characters, such as color and hairiness of the glumes and number of awns, while at the same time, in general, the intermediate type was preserved. In the 4th and 5th generations there were obtained forms resembling *T. vulgare* (LAUMONT, 1933).

All species of *Aegilops* cross with one another (G. M. POPOVA; OEHLER, 1934); in the majority of cases they produce sterile hybrids. Their genomes, as shown by cytological investigations, frequently are not homologous, which OEHLER explains by suggesting that species of *Aegilops* have undergone greater divergence in evolution than species of *Triticum,* and that evolution of *Aegilops* species has occupied a longer period than that of wheat species (OEHLER, 1934).

We must note the curious fact of the synthetic production of *A. triuncialis* by crossing *A. caudata* × *A. umbellulata* (O. N. SOROKINA).

As a rule, in hybridizing wheat with species of *Aegilops,* the *Aegilops* type is clearly dominant in the F_2; segregation into intermediate and wheat-like forms begins to be observed in the F_3.

The exchange of chromosomes and parts of chromosomes in distant hybridizations permits us to attempt experimental work in transferring valuable characters from parental species. GAINES in Pullman, Washington, has reported obtaining hybrid forms of wheat by crossing wheat with *Aegilops,* which were distinguished by immunity from fungus diseases. So far as we know, this is an isolated case; moreover the forms obtained were quite unsatisfactory for the purposes of practical breeding.

In use of species of *Aegilops* there is particular interest in obtaining amphidiploids. These may be still far from satisfactory for breeding purposes, but they are closer than the parental wild species of *Aegilops,* and it might be that by repeated backcrossing there could be obtained combinations suitable for breeding purposes.

All species of *Aegilops* cross with *Secale cereale* and *S. montanum,* particularly when *Aegilops* serves as the maternal parent. According to OEHLER, about 8% of seed are obtained from such crosses. The F_1 of *Aegilops* × *Secale,* as a rule, is sterile and the pollen does not develop. Backcrossing gives a very low percentage of success (0.008%). The genomes of rye and *Aegilops* are not even partially homologous; the chromosomes do not conjugate.

All species of *Aegilops* also cross with *Haynaldia villosa* Schur. Hybrids are obtained in this case when *Aegilops* is used as the maternal plant; about 3.5% of the blossoms produce seed. The F_1 is intermediate in character and sterile. Backcrossing has not succeeded (OEHLER). The Y genome of *Haynaldia* is not homologous with any genome of *Aegilops* species; the chromosomes do not conjugate.

Wheat-Agropyrum Hybrids:— Experiments in crossing the ordinary quack grass (*Agropyrum repens*) with wheat in order to obtain a perennial winter-resistant wheat, have been repeatedly made in different regions, but, either they gave no results, or as sometimes was the case, the described plants have not been true hybrids, but the result of self-pollination of imperfectly emasculated wheat used as the maternal form.

The question of hybridization of wheat with *Agropyrum* has been taken up anew in recent years in SSSR, beginning at the Saratov Breeding Station and later in the Omsk Institute of Grain Husbandry, in Odessa, and in other stations. Particularly extensive work along this line has been done by N. V. TSITSIN in the Omsk Institute of Grain Husbandry. Just as in earlier works of N. V. TSITSIN and at the Saratov Station (G. K. MEISTER, S. M. VERUSHKIN,[78] A. P. SHEKHURDIN), there was demonstrated the inability to cross ordi-

[78] VERUSHKIN: [Wheat-Agropyrum hybrids.] Selkhozgiz, Moskva, 1933. TSITSIN, N. V.: [The problem of winter and perennial wheat.] Sibirsk. Nauch.-Issled. Inst. Zern. Khoz., Omsk, 1933. MEISTER, G. K.: Summary (*l.c.*)

nary *Agropyrum repens* with wheat. Positive results, however, were obtained by using other species of *Agropyrum* in crossing, namely: *A. elongatum* Host., *A. glaucum* (Desf.) Roem. et Schult., *A. intermedium* (Host.) P. B., and *A. junceum* L., and also with *A. trichophorum,* which a number of authors relegate to the species *A. intermedium.* (The systematics of these species has not yet been worked out adequately, and sometimes different species appear under a single name.) Evidently within the limits of certain "species" there are forms with different chromosome numbers. The inadequacy of work on the systematics of *Agropyrum* evidently explains certain discrepancies in the work of the Saratov and Omsk Stations. All of the species enumerated, although ecologically and physiologically close to *A. repens,* are distinguished by winter hardiness and perennial form of life, and in a number of forms drought resistance and salt resistance; they are crossed with wheat quite easily when wheat is used as the maternal parent, and in the reverse cross as well, although in this case, the percent of success is lower. Despite the morphological differences which compel systematists to separate out *Agropyrum,* a number of species of the genus are quite easily crossed, sometimes giving 50 to 75% success. Not only does soft wheat cross with *Agropyrum,* but also hard wheat and other species (*T. turgidum, T. dicoccum*). *A. elongatum* is characterized by 35 chromosomes (haploid number), and *A. glaucum* by 21 chromosomes. N. V. TSITSIN obtained hybrids of *T. monococcum* with *A. glaucum* with 70.2% success. Particularly easy was the cross of wheat species with *Agropyrum elongatum* which has yielded a large number of hybrids. This species is also interesting for its resistance to smut and rust under conditions of western Siberia.

In the first generation the perennial form of life and general appearance of the *Agropyrum* are dominant, but some characteristics are taken over from wheat. As a rule the first generation appears to be entirely sterile (G. K. MEISTER, S. M. VERUSHKIN). N. V. TSITSIN succeeded in finding among the masses of sterile plants of the first generation from the cross of *T. vulgare* × *A. elongatum* 60 plants with some fertility, showing on the average 2 grains per head..

For obtaining further generations both the Saratov and Omsk stations resorted to repeated pollination of the hybrids of the first generation with wheat of the parental form. Thus TSITSIN, in repeated pollinations of the hybrids *T. durum* and *T. vulgare* × *A. elongatum* with wheat pollen, from 3023 pollinations obtained 209 grains or 6.5% success; in another combination, pollinating the hybrid *T. vulgare* × *A. glaucum* with wheat pollen, from 2218 blossoms he obtained 89 grains or 4% success. The Saratov Station found that in cases of such hybrids pollinated by wheat the percent of success was 1.27 or even 1.87.

In general the percent of success from repeated pollination was somewhat higher than with rye-wheat hybrids repeatedly pollinated by wheat, where, according to the work of the Saratov station, on the average there is obtained only a fraction of a percent of success. Reciprocal crosses in the first generation gave identical plants.

The species *A. cristatum, A. sibiricum, A. ramosum, A. desertorum, A. tenerum, A. gmelini,* and *A. elymus,* according to the experiments of the Omsk and Saratov Stations, do not cross with wheat.

The highest percent of success in crossing was obtained with *T. durum* × *A. elongatum* and *T. vulgare* × *A. glaucum.* The percent of germinating seed in these hybrids was always high (N. V. TSITSIN).

The Saratov and Omsk Stations (N. V. TSITSIN and S. M. VERUSHKIN)

have followed segregation to the fourth and, in some cases, to the 7th generation. Hybrids of *Agropyrum,* when repeatedly crossed with wheat, in later generations showed a sharp segregation with a great amplitude of variability, which is customary in distant crosses. In the third and fourth generations were found forms with new characters reminding one of other species. N. V. Tsitsin noted the appearance of squareheads, compact heads, branched heads, segregates of the *durum* type with different degrees of compactness, and even some forms resembling *Aegilops.* What was most significant was the appearance of wheat-like forms with valuable agricultural characters of *Agropyrum,* such as winter-resistance, the perennial habit, and resistance to diseases. (*A. elongatum* is resistant to loose smut, rust, and powdery mildew). In the great majority of plants the heads of the second and particularly the third generation, were close to wheat in type. In crossing wheat with hybrids of the second generation there was obtained a rather high degree of success, averaging 50% (N. V. Tsitsin).

S. M. Verushkin[79] (1935) noted that whole plots in the older generations of hybrids were resistant to rust and smut. Among them were a number of wheat types which undoubtedly have practical interest. Promising forms have been obtained by crossing hard wheats with *Agropyrum intermedium* and *A. trichophorum.*

The first generation of hybrids of wheat with *Agropyrum,* when repeatedly crossed with wheat, have a tendency to cross-pollination, which is a property of *Agropyrum.* However, in segregation in later generations there separate out forms which have a greater and greater tendency to self-pollination. With later generations there is an increase in yield, and thus we can see the possibilities of solving some attractive problems in creating perennial wheat, wheat with winter resistance, and varieties of wheat that may be grown on dark alkaline soil (a characteristic of certain forms of *Agropyrum*). The possibility of vegetative reproduction of *Agropyrum* by using pieces of rhizomes or by dividing plants into many pieces (up to 300) will considerably facilitate breeding work and aid the creation of entirely new forms.

The rank development of the vegetative mass of hybrids of the first generation and certain plants of later generations contributes to our basic problem of developing new forage plants. Some of the hybrid plants have very well developed root systems, the first generation sometimes even surpassing *Agropyrum* in this respect. This renews our interest in creating drought-resistant spring and winter forms and perennial forms.

The perennial habit of life evidently is dominant, particularly in crosses with winter wheat. In the third generation there separate out perennial forms with the wheat type of head and grain, the latter approaching normal wheat in absolute weight. The segregates also include valuable forms with respect to quality of grain. Many of these segregates can be distinguished from wheat plants only with difficulty. The type of heads of many forms in the third generation places them within *T. vulgare,* but they still continue to segregate (Verushkin). In some cases the wheat type of plant is combined with high yield, self-pollination, and the perennial form of life (Verushkin). It is interesting to note also the appearance of annual hybrids in the third generation, which are distinguished by high productivity with absolute weight of grain equaling that of wheat.

In the progeny of hybrids from crosses of spring wheat with *A. elongatum* there have been found a considerable number of typical winter forms with

[79] Verushkin, S. M., 1935. [Hybridization of wheat with *Agropyrum.*] NKZ-SSSR. Saratov Sel-Genet. Stants., Gosizdat, Saratov, 38 pp.

heads resembling wheat. In 1934 the Omsk Station alone had in its fields about 50,000 plants in the 5th generation of wheat-*Agropyrum* hybrids. Extensive work has also been done in the Saratov Station.

The first generation of the hybrids are inclined to natural pollination by wheat, which may be used practically.

B. A. VAKAR and his co-workers have studied the cytology of the wheat-*Agropyrum* hybrids (1934). The facts disclosed have great interest. The study of meiosis in the F_1 hybrids of wheat × *Agropyrum elongatum* and *A. glaucum* has shown that this has more of the character of the type of meiosis observed in interspecific wheat hybrids than of the type of meiosis in crosses between genera, *e.g., Triticum* and *Secale* or even *Aegilops*. The most significant fact is the presence of a large number of homologous chromosomes in wheat and *A. elongatum* or *A. glaucum*. The maximal number of bivalent chromosomes in the reduction division in F_1 hybrids of *T. vulgare* (21) × *Agropyrum glaucum* (21) equals 14; 7 chromosomes of *T. vulgare* and 7 chromosomes of *A. glaucum* fail to conjugate, giving 14 univalents. Sometimes the number of bivalents was less, the most frequent number being 10. Here the union of chromosomes was not ring fashion, as is usual in hybrids of wheat with species of *Aegilops* or rye, but lengthwise, which also shows the greater similarity of some of the wheat chromosomes with those of the *Agropyrum* species tested, particularly *A. elongatum*. There is not excluded the possibility of the occurrence of autosyndesis between chromosomes of the same haploid assortment. VAKAR's conclusions were confirmed by the investigations of A. A. SAPEHIN. Evidently some forms of *Agropyrum* give a high percentage of bivalents in crosses with wheat. In VAKAR's opinion, in all probability there is conjugation between the 7-chromosome genomes A and B of wheat with the chromosomes of 2 genomes (of 7 chromosomes each) of *Agropyrum*. In the investigated species of *Agropyrum,* as in wheat, the chromosome number appears to be a multiple of 7: in *A. elongatum* 70, in *A. glaucum* 42 (in somatic cells).[80]

The number of chromosomes in the F_1 hybrids in the metaphase and anaphase of the first division (computing them as univalents) always equals the sum of the haploid number of chromosomes of both parents; in the F_1 of *T. vulgare* (21) × *A. glaucum* (21) it equals 42 (2 n), in *T. vulgare* (21) × *A. elongatum* (35) it equals 56, and in the F_1 hybrids of *T. durum* (14) × *A. elongatum* (35) it equals 49.

In meiosis the regular position of the bivalent chromosomes at the pole, and the equatorial position of the univalents after separation of the bivalents, reminds one of the behavior of interspecific hybrids of wheat. The regularity in the metaphase plate also indicates the comparatively balanced chromosome assortment in wheat-*Agropyrum* hybrids (B. A. VAKAR, 1934). A different behavior of chromosomes is usually observed in intergeneric hybrids. The pollen in wheat-*Agropyrum* hybrids (F_1), although in general entirely sterile, contains occasional normal-appearing pollen grains which may be functional in fertilization. The finding by TSITSIN of some fertile plants in the F_1 serves as evidence of this.

[80] In a later work (1935) B. A. VAKAR found that hybrids of *Agropyrum elongatum* with *Triticum vulgare* can form 21 bivalent chromosomes, which testifies to a significant relationship between these species of plants. VAKAR assumed that all the chromosomes of soft wheat, totalling 21, conjugate with 21 chromosomes of *Agropyrum elongatum, i.e.,* that there are present in the whole assortment of chromosomes of *A. elongatum* chromosomes of all three genomes of soft wheat. The remaining 14 chromosomes of *A. elongatum* also may conjugate among themselves (autosyndesis), and thus sometimes form zygotes with 28 pairs of chromosomes.

The cytological facts demonstrated by VAKAR indicate that the species *A. glaucum* and *A. elongatum* are related more readily to the genus *Triticum* than to the genus *Agropyrum*. We note, however, that in all cases the ecology of species of *Agropyrum* is so very distinct from that of wheat that it would be premature to combine them with wheat.

All of the facts set forth testify that some species of *Agropyrum* evidently stand genetically closer to wheat than was believed up to this time. The large number of species within this genus, and the possibility of a great variety of combinations opens up new perspectives.

The facts that have been determined give hope of a new approach to the problems of wheat under the conditions of our rigorous continental climate. The vegetative reproduction of *Agropyrum* broadens further the possibilities of breeding.

The role of the individual parental forms used in crossing is very great. Thus two pure lines of hard wheat, 0432 and 010, were pollinated with the same form of *A. intermedium* and gave in the first case 90% of seed set and in the second, only 2%. In the reverse case, in pollinating one constant hybrid of hard awnless wheat with two different forms of *A. intermedium,* in one case was obtained 8.5 and in the other 84% successful pollination (G. K. MEISTER). This work must be carried out on a broad scale in view of the complexity of the process of segregation and the necessity of completely eliminating sterility. The problem of combining in one variety the majority of valuable characters when *transferring them from two different genera or even from different widely-separated species* is a very complex matter, theoretically requiring much persistence, an extensive scale of work, and a relatively large number of generations in order to obtain the desired goal. The high requirements in a wheat variety with respect to grain and at the same time many other characters, requires combinations that theoretically would appear very rarely. Looking over our F_4 and F_5 generations, there appears to be a particular need for improving the form of the grain. Repeated crossings to add valuable characters will evidently play a most important role in obtaining these combinations.

In further investigations of *Agropyrum*-wheat hybrids we must consider the complexity of the process of segregation and direct our attention to means for more rapidly creating the necessary combinations. In any case, in the light of the facts that have thus far been determined, we have a problem that has exceptional interest both theoretically and practically.

The genus *Agropyrum* has included in its evolution the continents of Asia, Europe, and North America, and consists of many species and forms, which requires a planned, many-sided study with inclusion of new species in crosses with wheat.

Even at the present time we may consider that by crossing wheat with *Agropyrum* we have obtained new valuable forage plants which in itself contributes to an important problem for West Siberia and the southeastern European part of SSSR.

Wheat-Haynaldia Hybrids:— All species of cultivated wheat cross with the Mediterranean species *Haynaldia villosa* (or *Triticum villosum*) particularly when wheat is used as the maternal parent. The percent of success is usually very small. Both in our experiments (with *Triticum vulgare*) and in the crosses of CHERMAK, OEHLER, and others, the number of grains obtained from pollinated plants did not exceed 1-2%. In external appearance the F_1 hybrids are intermediate, with wheat characteristics dominating. The F_1 hybrids have sterile pollen. Backcrosses, as a result of anomalies in the reduction division, give poor percentages of seed set (according to OEHLER 0.06%).

The Y genome of *Haynaldia* is not homologous with the genomes ABC of wheat, and in crosses with wheat all the chromosomes in the F_1 are univalent. The male gametes are often not reduced. CHERMAK obtained fertile, constant amphidiploids by crossing *Triticum turgidum* with *Haynaldia villosa,* analogous in behavior to *Aegilotricum* and *Triticale.*

Thus far there have not been obtained hybrids of *Haynaldia* with cultivated rye, either when the rye was used as maternal parent or in the reverse combination.

Hybrids Combining the Characteristics of Three or More Species and Genera:— Genetic-cytological investigations have brought out the very important fact of autosyndesis in wheat, and the possibility of its use for further work in interspecific and intergeneric hybridization. Some assortments of chromosomes, *i.e.,* genomes, are similar and homologous in different species and even genera of cereals.

Einkorns are characters by genome	A
Triticum timopheevi is characterized by genomes	AG
Species of the group of hard wheats, genomes	AB
Species of the group of soft wheats, genomes	ABC
Rye—*Secale cereale,* genome	X
Aegilops cylindrica, genomes	CD
Other species of *Aegilops,* genomes	DEFGS
Agropyrum glaucum, genomes	ABZ
Haynaldia villosa, genome	Y

Genomes indicated by a given letter are partly or fully homologous, *i.e.,* they form bivalents in conjugation. Genomes designated by different letters, when combined, result in irregularities in the reduction division; the chromosomes do not conjugate, and usually such hybrids are sterile, but in this case amphidiploids and the inclusion of pairs of genomes may result in original, fertile combinations which have theoretically interesting possibilities from the standpoint of experimental procedure and species formation.

Aegilops cylindrica, according to the data from cytological investigations, has one genome, *i.e.,* one set of 7 chromosomes which is common to *Triticum vulgare,* while its other genome of 14 chromosomes is present in *Aegilops ovata* (cf. the interesting scheme of similarity of genomes of wheat and *Aegilops* species in the work of H. C. AASE, 1930[81]).

V. N. LEBEDEV (1930-1933) has studied the progeny of soft wheat (21 chromosomes) crossed with rye (7 chromosomes) and then backcrossed with rye, and found in the progeny, as has been pointed out above, 28-chromosome forms (2 n) containing a full somatic assortment of rye chromosomes (14) plus 14 chromosomes of wheat, *T. vulgare.* The forms obtained were morphologically intermediate between rye and wheat and were distinguished by their comparative fertility, normal reduction division, and good pollen (more than 70%). The 14 bivalents formed in this case, which resulted in normal zygotes, were due to the conjugation (7 + 7) of non-homologous chromosomes of the haploid assortment of soft wheats with 7 pairs of the rye assortment.

The occurrence of conjugation between different chromosomes of a single haploid assortment (autosyndesis) was also found in other plants.

LEBEDEV holds that species formation in soft wheat proceeds through two principal stages: the formation of tetraploid species, and the production of hexaploid species as a result of hybridization. Recent data of V. A. PODDUBNA

[81] H. C. AASE. Cytology of hybrids. Research Studies of the State College of Washington 2 (1), 1930.

on morphological differences of chromosomes among the 14-chromosome group (haploid number) have cast some doubt on this opinion of LEBEDEV.

The absence, in a majority of cases, of bivalents in the meiosis of wheat-rye hybrids of the first generation, in LEBEDEV's opinion, testifies to the absence, in the chromosome collection of soft wheats, of rye chromosomes which would have to be present if, as G. K. MEISTER assumes, soft wheats originated from some species of the group of hard wheats and rye with hybridization and the addition of chromosomes. The causes underlying the possibility or impossibility of conjugation of chromosomes are still little known. It is natural to assume that in cases of conjugation of genomes there must be phylogenetic homologies (relationships).

The fact of autosyndesis of chromosomes in soft wheats has been noted by WINGE (1924), NILSSON-LEISSNER (1925), and HASKINS (1928), and evidently it occurs in a number of crosses, particularly when one of the parents has a large number of chromosomes.

According to the investigations of LEBEDEV, autosyndesis involves greater or lesser numbers of chromosome pairs, depending on the choice of parental forms of wheat, *i.e.*, different wheat races incline to autosyndesis to different extents. From this he concludes that there is a similarity in the two genomes of soft wheats. In his opinion the occurrence of autosyndesis in wheat indicates a high degree of relationship between the wheat chromosomes of a single haploid assortment. The third wheat genome, which remains in a univalent condition, LEBEDEV assumes must be distinct from the two genomes which conjugate with each other.

TSCHERMAK (1925) has observed natural hybrids between three genera: *Aegilops, Triticum,* and *Secale,* which he has named *Aegilotricale.* LEIGHTY and SANDO have obtained an artificial hybrid between *Aegilops ventricosa* × *Triticum turgidum* × *Secale cereale, i.e.,* a three-generic hybrid, which they have called *Aegilotriticale.* The hybrid has inherited morphological characters such as hairiness of the stem under the heads, form of glumes, etc., from all three genera. The hybrid is entirely sterile, nor will it cross with either *Aegilops ventricosa* or *Secale cereale.*

Dr. DONCHO KOSTOV has recently introduced the new conception of the use of the method of *triple* species hybrids of wheat for obtaining combinations of valuable characters occurring in distantly related species.

He has found that hybrids of *T. dicoccum* × *T. monococcum* when crossed with *T. vulgare* in certain combinations gave three-genome hybrids with 42 somatic chromosomes. 14-chromosomes were inherited from *T. dicoccum,* 7 from *T. monococcum,* and 21 from *T. vulgare.* These hybrids were partly fertile. It is possible that some of the combinations of this kind may be valuable materials for breeding, particularly for backcrosses with *T. vulgare.* Investigations of KOSTOV, GOODSPEED, EGIZ, and others, have shown in the case of tobacco, the possibility of obtaining such types that are entirely fertile with a balanced chromosome apparatus. Moreover, there has resulted the very likely hypothesis of the origin of ordinary cultivated tobacco by a combination of genomes of several wild species of tobacco (for example *Nicotiana rusbyi* and *N. sylvestris*).

Dr. KOSTOV has proposed the possibility of combining, for example, valuable qualities of *T. monococcum,* such as immunity from rust, with the group of hard and soft wheats, by using non-reduced gametes of *T. monococcum* for fertilizing normal gametes of emmer or soft wheat. For example, in his experiments the hybrid of *T. turgidum* (n) × *T. monococcum* (2n) was almost fertile. The hybrid of *T. vulgare* (n) × *T. monococcum* (2n) was partly

fertile. In the progeny of the latter cross there appeared almost completely fertile plants; among them was a series of plants with 28 chromosomes and almost normal reduction division. For the same purpose he recommends the use of *T. timopheevi* Zhukov.

The method of Dr. KOSTOV evidently requires a large number of crosses, since the majority of such combinations appear to be almost sterile, but the possibility remains of attempting to create such combinations by suitable choice of genomes, by use of cyclic crossings, and by bringing into the hybridization a diversity of species.

In any case the breeder must consider the possibility of a regrouping of valuable genomes represented by the groups of 7 chromosomes in species of wheat and closely related genera. By this means there probably will be obtained in the future interesting new forms.

The investigations of L. N. DELONE and his co-workers have resulted in obtaining other three-genome hybrids combining genomes of hard wheat, rye, and soft wheat, in which the forms obtained were partly fertile. Rye, like einkorn, has 7 chromosomes, but these are different from the chromosomes of einkorn. It is interesting that, although the hybrids of rye with soft wheat (F_1) have very low fertility with a majority of abnormal pollen grains, when the genome of soft wheat is added the hybrids have high fertility.

MÜNTZING (1935) at the Svalöf Station has obtained a partly fertile hybrid of *T. turgidum* × *Secale cereale* × *T. vulgare*. The chromosomes in this hybrid, in the first metaphase consist of 14 bivalents and 14 univalents combined ($14_{II} + 14_{I}$). This chromosome combination clearly shows the non-homology of the chromosomes of rye with those of soft wheat, which in turn indicates, in MÜNTZING's opinion, the incorrectness of G. K. MEISTER's view on the origin of soft wheat by a crossing of emmer (*T. dicoccum*) and rye. The hybrid obtained was a phenotypic combination of properties of all three parents according to the morphology of the heads.

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A number of investigators (GAINES, KIHARA, B. I. VASILEV, and others) have found haploid forms in wheat some of which have been obtained as a result of distant hybridization and others by X-ray treatment of pollen before fertilization. Such pollen permits the parthenogenetic development of embryos. By X-ray treatment there were obtained, for example, many haploid forms (16) in *T. monococcum* (KATAYAMA, 1934). The haploid forms, as a rule, are distinguished by lower and weaker growth and sterility. They have been obtained in all three chromosomal groups of wheat: in einkorns, *T. persicum* (B. I. VASILEV), *T. durum* and *T. compactum* (GAINES and AASE), and in *T. vulgare*. If, in such haploid forms, it were possible to double the chromosome apparatus, we would obtain ideal pure lines and restore fertility.

Mutations in Wheat:— Along with natural and artificial hybridization in the origin of forms of wheat, mutation also has significance. The present diversity of wheat is evidently due both to mutations and to a frequent occurrence, in the past and at present, of the process of hybridization.

In the literature may be found a large number of descriptions of natural mutations in wheat; an example is the appearance of awned forms from awnless parental forms. A particularly frequent case is the so-called speltoid mutation which was first described in detail by NILSSON-EHLE and later observed and studied by many authors (LINDHARD, ÅKERMAN, HÄKANSSON, KAJANUS, HUSKINS, WINGE, FILIPCHENKO, DELONE, and others). Almost every breeding station has observed cases of the appearance of such speltoid mutations.

Such mutants show a number of characters of *T. spelta*, such as abbreviated glumes, loose heads, and persistent coverage of the grain. Sometimes the mutation has involved only one side of the head, *i.e.*, we are dealing with a chimaera. Often mutation involves a whole complex of characters. In the majority of cases only one gamete mutates, and hence the mutation appears to be heterozygous.

A study of segregation shows that in these cases there usually is mutation of one gene but it may have pleotropic effects on a number of characters. Biologically such speltoid forms, as NILSSON-EHLE has shown, are characterized by some reduction in productivity. In recent years the speltoids have been studied cytologically. WINGE (1924) and HUSKINS (1928) have explained the behavior of speltoid mutations as a result of chromosomal aberration, a consequence of irregularity in the distribution of chromosomes. HUSKINS found that different types of speltoids are characterized by different numbers of chromosomes. In type A the number of chromosomes is normal (42). Heterozygous speltoids of type B have 41 chromosomes, *i.e.*, are monosomic. Type C has 43 chromosomes (trisomic) and derived from it are homozygous speltoids with 44 chromosomes (tetrasomic). Evidently in a number of cases the situation is more complicated (VASILEV, 1929).

A number of authors have noted the appearance of club mutations (VILMORIN and others). FRUWIRTH has observed vegetative mutations, for example the formation on a plant of awnless wheat of individual tillers with awned heads.

Speltoid vegetative mutations in *T. vulgare* have been found by M. G. TUMANYAN in Armenia.

In comparing wheat with other plants, all of the investigators have observed that wheat evidently mutates less frequently than other plants such as snapdragon, barley, or corn. Evidently vegetative mutations are most common in wheat. M. G. TUMANYAN has found very frequent vegetative mutations in Armenia, particularly in soft and club wheats.

The discovery by Dr. MULLER of the possibility of inducing the mutation process by using X-rays has stimulated work in obtaining artificial mutations in wheat. Extensive work of this sort has been done in recent years, particularly in the Missouri Agricultural College by Dr. STADLER and in Russia by L. N. DELONE, A. A. SAPEHIN, and also at the All-Union Institute of Plant Industry. X-ray treatment results in many mutations in various directions. The qualitative nature of these changes is quite varied. In the first place, there are gene mutations which have particular interest for the breeder; in the second place, the great majority of new types have chromosomal aberrations; and finally, distinct from the two preceding types, there are occasionally found major physiologic changes produced by X-rays, such as acceleration of growth, changes in chlorophyll, etc., obtained by irradiating the seed. Most frequently there occurs a fragmentation or a translocation of chromosomes. Univalents in the reduction division are very common; rarely there occur trivalents and quadrivalents. Often one finds anomalous reduction divisions with chromosomes strewn about at random (SAPEHIN, 1934). The chromosomal aberrations are accompanied by low viability, and accordingly, in the second generation few individuals survive. In the second year the genic mutants are the ones which principally survive. As a result of the effects of X-rays we usually find in soft wheat a motley first generation developing from the X-ray treated sexual cells, including a majority of speltoids, many of which are sterile. The second generation is comparatively uniform. Other forms of wheat, as a re-

sult of X-ray treatment, produce non-uniform mutations in the first generation (A. SAPEHIN).

In hard wheats the diversity of forms in the first generation is smaller; there is observed a limited number of types: with soft glumes, elongated teeth, and small or elongated glumes (A. SAPEHIN). The majority of these aberrants are sterile. The second generation, as in soft wheats, is also uniform, and the new types consist of genic mutations.

The chromosomal aberrations, in the majority of cases in both hard and soft wheats, are sterile.

The genic mutations are principally recessive, and as a rule have little viability; frequently the mutants are monstrosities; many of the mutants, to greater or less degree, are sterile, but there occur rare cases of valuable mutations, for example A. A. SAPEHIN in the first of his works, has obtained highly cold-resistant forms of winter wheat in this way. L. N. DELONE is inclined to regard a number of the wheat mutations as valuable forms.

STADLER has observed a law in the appearance of mutations in wheat and oats, namely that species with small numbers of chromosomes mutate more frequently than species with larger, multiple numbers of chromosomes. This concerns genic mutations. STADLER associates this rule with the presence of double and triple numbers of genes in species with larger numbers of chromosomes. The results of experiments carried out by the Genetics Section of the Institute of Plant Industry (G. G. BATIKYAN) cast some doubt on this assumption of STADLER's. In any case, STADLER's law cannot apply generally to the genic composition of wheat with many chromosomes.

Investigations in this field are in progress, and it is too early to recount the results, but we must note that from the breeder's point of view, the great majority of forms obtained in this manner have little biological value. Most of the forms are inferior to the parents. For obtaining useful results it is necessary to carry the work out on a broad scale, observing the mutations through a number of generations, since valuable forms may segregate out in the later generations because, in all probability, as in natural mutations, most of the cases of mutations involve a single gamete.

Even such investigators as STADLER and MULLER, who have worked particularly on the use of X-rays for obtaining new forms, consider that in work with the cereals hybridization is still the more useful procedure. Recently A. A. SAPEHIN (1934) has come to the same conclusion, pointing out that although in rare cases one may obtain useful mutations, in wheat the basic artificial means of producing new forms is by hybridizing different geographic races and closely related species. L. N. DELONE (1934)[82] attaches more significance to mutations in wheat, both natural and artificially obtained.

We still do not have definite information concerning the effects of other factors on the artificially obtained mutations in wheat. It is possible that ultraviolet light, which penetrates deeply into cells, may be used for this purpose. In any case, this field still needs to be worked out. Considering the great number of wheat species and the great diversity of ecological-geographic types, the most promising procedure at present appears to be the creation of new forms by hybridization. Theoretically the study of mutations in wheat is most interesting because otherwise it would be difficult to explain the diversity of original forms. It is possible that by more delicate procedures there may be obtained valuable mutations.

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[82] L. N. DELONE: [Experimentally produced mutations in wheat.] Ukraine Inst. Rastenievod., Kharkov, 1934.

M. S. NAVASHIN has recently shown that old seed of plants (particularly of rye) may exhibit chromosomal aberrations or genic mutations.

The Extent of Work Necessary in Practical Wheat Breeding:— The practice in breeding stations differs respecting the extent of crossing necessary to produce hybrids combining desired characters.

In crossing wheat species of different chromosome numbers, the work must be sufficiently extensive so that in the F_2 there will be thousands of plants for analysis. At the Odessa Breeding Station the practice includes use of large F_2 and F_3 populations, ranging up to 1.5-2 millions of hybrid plants in crosses between hard and soft wheats.

Ordinarily, in recent times, breeding stations attempting to produce practically valuable hybrids carry out the work on a great scale in crosses of 28- and 42-chromosome wheats. In crosses of einkorns with other species, it is impractical to carry out the work on such an extent because of the great amount of sterility in the F_1.

At the Svalöf Station, and also at the Müncheberg Institute of Breeding in Germany, for crossing different wheat species of the same chromosome number, and for crossing different geographic races, it is considered necessary that the work be carried out on a large scale providing, in the second generation, tens of thousands of plants. The directors of these institutes (NILSSON-EHLE, ÅKERMAN) consider that this scale of work is modest in view of the many genes distinguishing the parental forms and the small probability of the appearance of desired combinations. For example, to improve the bread-baking quality of Swedish wheats at the Svalöf Station, Russian soft wheat varieties have been crossed with the best breeding varieties of Sweden. Experience has shown that for winter wheat no less than 10,000 plants in the F_2 are necessary in order rapidly to obtain the desired hybrid combinations.

The more closely related the parental forms are with respect to their gene complexes, the less extent of work is required for obtaining necessary combinations. In this matter much depends on the purpose of breeding. If the desired character, for example bread-baking quality, is governed by many genes, then the extent of the work must be correspondingly greater.

A number of authors (YU. A. FILIPCHENKO, T. K. LEPIN), consider that in hybridizing wheat the F_2 may be a rather small generation, since they direct all attention to detailed investigation in the F_3 and F_4. They separate out of the F_2 extreme variants with respect to combinations of the desired agricultural characters, and from them establish an F_3. The same practice is followed in later generations. In this way there may rather rapidly be obtained extreme variants which are practically constant.

The procedures of this school of workers are based principally on a study of the behavior of morphological quantitative characters in soft wheat crosses.

We have shown that in crosses of species with different chromosome numbers it is more correct to obtain the largest possible number of plants in the F_2. In such crosses there are many lethal gametes, and consequently the probability is much reduced that the necessary valuable combinations will appear and this requires an extensive F_2 for securing such combinations.

In crossing different geographic races which differ sharply in their constitution, as well as in crossing species with the same chromosome numbers, but which are quite distinct, in order to obtain all wanted combinations there must be a large number of plants in the F_2 in order that valuable forms may be selected directly from it. In crossing comparatively closely related forms to obtain extreme variants for agricultural purposes, attention should be given

to the selection of extreme variants in the F_2 from comparatively small numbers of plants, with selection continued in the F_3 and F_4. The Svalöf Breeding Station, as well as many other breeding institutes, when dealing with crosses of closely related plants, work on a scale involving thousands of plants in the F_2.

The history of practical breeding shows us that valuable forms have frequently been selected from comparatively late generations. The improved Canadian variety "Marquis" was obtained in this way. In addition to a large number of plants in the F_2, it is also necessary to study the progenies of later generations, considering the possibility of the late appearance of rare but valuable combinations.

The history of breeding in the past shows us that valuable varieties have been obtained from work on a rather small scale, but this has involved a correspondingly large number of generations and long time. Unfortunately, in the majority of reports of experiment stations and breeding firms there is no exact documentation of the extent of the work or of the segregation ratios.

We must call attention to the simplified bulk method practiced by ERWIN BAUR and other breeders, and particularly by commercial firms. In this method, when wheat species of different chromosome numbers are crossed, the hybrid progeny is planted without selection and propagated for a number of years. The seed of the plants is mixed every year, and only at the fifth or sixth generation is individual selection begun. Beginning with the second generation, the plants are subjected to natural selection, which eliminates forms of little value, conserving those which are best adapted to the given conditions and have the highest yields, and which consequently tend to predominate in the later generations.

For orientation in the process of segregation, particularly when dealing with new, unstudied combinations of unknown genetic relationships, it is more useful to subject at least part of the F_2 and F_3 generations to individual genetic study. Intelligent breeding based on the data of genetic analysis makes possible wiser selection.

The Ideal Wheat Variety:— Having surveyed the generic, specific, and varietal potentials of wheat and the theoretical possibilities of creating new forms of wheat, we pass to the question of practical breeding, and first of all we must consider the type of wheat at which the breeder is aiming.

Present day requirements for wheat are very great. The long historical period during which this plant has been cultivated, the growing significance of wheat in the nutrition of the world's populations, and the greater and greater quality requirements of the world wheat market present new problems to the breeder.

In the development of wheat breeding, a great role has been played in the past, and continues to be played at present, by socio-economic changes. The breeding of wheat is inseparable from the economics and technology of agriculture. The development of irrigation in old and new agricultural regions has stimulated the production of new types of wheat which differ from the original wild prototypes of the prairies. The expansion of populated areas in the Old World, the development of American and Australian agriculture, the clearing of great forested areas in Europe, and the extension of agriculture to the north have been accompanied not only by an increase in the cultivation of wheat, but also by the development of new types of varieties.

During the last decades the requirements for wheat grain have been determined by the demands of the milling and baking industry. The capitalistic

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Ordinarily, in recent times, breeding stations attempting to produce practically valuable hybrids carry out the work on a great scale in crosses of 28- and 42-chromosome wheats. In crosses of einkorns with other species, it is impractical to carry out the work on such an extent because of the great amount of sterility in the F_1.

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The more closely related the parental forms are with respect to their gene complexes, the less extent of work is required for obtaining necessary combinations. In this matter much depends on the purpose of breeding. If the desired character, for example bread-baking quality, is governed by many genes, then the extent of the work must be correspondingly greater.

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The procedures of this school of workers are based principally on a study of the behavior of morphological quantitative characters in soft wheat crosses.

We have shown that in crosses of species with different chromosome numbers it is more correct to obtain the largest possible number of plants in the F_2. In such crosses there are many lethal gametes, and consequently the probability is much reduced that the necessary valuable combinations will appear and this requires an extensive F_2 for securing such combinations.

In crossing different geographic races which differ sharply in their constitution, as well as in crossing species with the same chromosome numbers, but which are quite distinct, in order to obtain all wanted combinations there must be a large number of plants in the F_2 in order that valuable forms may be selected directly from it. In crossing comparatively closely related forms to obtain extreme variants for agricultural purposes, attention should be given

to the selection of extreme variants in the F_2 from comparatively small numbers of plants, with selection continued in the F_3 and F_4. The Svalöf Breeding Station, as well as many other breeding institutes, when dealing with crosses of closely related plants, work on a scale involving thousands of plants in the F_2.

The history of practical breeding shows us that valuable forms have frequently been selected from comparatively late generations. The improved Canadian variety "Marquis" was obtained in this way. In addition to a large number of plants in the F_2, it is also necessary to study the progenies of later generations, considering the possibility of the late appearance of rare but valuable combinations.

The history of breeding in the past shows us that valuable varieties have been obtained from work on a rather small scale, but this has involved a correspondingly large number of generations and long time. Unfortunately, in the majority of reports of experiment stations and breeding firms there is no exact documentation of the extent of the work or of the segregation ratios.

We must call attention to the simplified bulk method practiced by ERWIN BAUR and other breeders, and particularly by commercial firms. In this method, when wheat species of different chromosome numbers are crossed, the hybrid progeny is planted without selection and propagated for a number of years. The seed of the plants is mixed every year, and only at the fifth or sixth generation is individual selection begun. Beginning with the second generation, the plants are subjected to natural selection, which eliminates forms of little value, conserving those which are best adapted to the given conditions and have the highest yields, and which consequently tend to predominate in the later generations.

For orientation in the process of segregation, particularly when dealing with new, unstudied combinations of unknown genetic relationships, it is more useful to subject at least part of the F_2 and F_3 generations to individual genetic study. Intelligent breeding based on the data of genetic analysis makes possible wiser selection.

The Ideal Wheat Variety:— Having surveyed the generic, specific, and varietal potentials of wheat and the theoretical possibilities of creating new forms of wheat, we pass to the question of practical breeding, and first of all we must consider the type of wheat at which the breeder is aiming.

Present day requirements for wheat are very great. The long historical period during which this plant has been cultivated, the growing significance of wheat in the nutrition of the world's populations, and the greater and greater quality requirements of the world wheat market present new problems to the breeder.

In the development of wheat breeding, a great role has been played in the past, and continues to be played at present, by socio-economic changes. The breeding of wheat is inseparable from the economics and technology of agriculture. The development of irrigation in old and new agricultural regions has stimulated the production of new types of wheat which differ from the original wild prototypes of the prairies. The expansion of populated areas in the Old World, the development of American and Australian agriculture, the clearing of great forested areas in Europe, and the extension of agriculture to the north have been accompanied not only by an increase in the cultivation of wheat, but also by the development of new types of varieties.

During the last decades the requirements for wheat grain have been determined by the demands of the milling and baking industry. The capitalistic

development of the milling and baking industry of western Europe, the change from the feudal regime with its primitive windmills and millstones, have created new requirements for wheat. The invention of the rolling mill has changed the requirements for grain consistency. The increasing centralization of the grain industry has brought about basic changes in the requirement for wheat assortments. The development of the world grain trade, the competition of capitalistic regions among themselves, and shipments to a world market by Canada, Argentina, and Australia, have introduced new and great changes in the conception of wheat standards. The invention in the second half of the 19th century of the rolling mill in Hungary, resulting in the production of soft winter wheat with vitreous grain, has brought about great changes in the world geography of cultivated wheats. Rolling mills became widespread at the end of 1870's in the U. S. A. Vitreous wheats, which had been avoided in the time of the older mills, began to be preferred by the milling and baking industry. Instead of the mealy wheats which were principally cultivated in the past, agriculture had to turn to the culture of soft wheats with hard vitreous grain, which the milling and baking industry required. Thus hard wheat (*T. durum*) which requires special milling, rapidly became replaced, even in the basic regions of culture of this species along the shore of the Mediterranean Sea. It has survived here principally among the Arabian population who use it for making so-called "kuskus" *i.e.*, grain that is moistened after milling, somewhat fermented, and then dried and used as rice, and also for making macaroni. The acreage under the mealy English wheat (*T. turgidum*) has shrunken in the last decade, and this is now grown only for production of poultry feed where the grain quality requirement is low.[83]

Industry today requires wheat grain with a high protein content, which gives flour of the best baking quality. Vitreous wheat, which the mills avoided in the past, has begun to receive high premiums in the world market. The simplification of protein analysis based on the method of the Danish chemist KJELDAHL (1883) has made possible the rapid testing of grain for protein.

The increase in the baking industry associated with the growth of cities has particularly raised the requirement for grain quality. Chemical laboratories have become essential parts of the baking industry. Flour with a high percentage of protein absorbs and holds more water and produces better bread than flour with low protein.[84] Flour with a high protein content holds its form better. In a number of locations there have been worked out requirements for determining the type and form of the bread loaf. Frequently on the London and New York markets flour with high protein content is valued 20-30% higher than flour with low protein content.

At the same time it is natural that we find efforts at breeding for a combination of high quality grain and high yield.

The mechanization of agriculture during the past decade has brought new requirements for varieties. Lodging of grain in the field was not a particular hazard when grain was harvested by hand with a sickle. The appearance of harvesting machines, binders, and then the combine, which has become particularly widely used in Argentina, have presented new problems to the wheat breeder. Varieties that are produced by the breeder today must be at one time suitable for agriculture, milling, and baking. These requirements fre-

[83] For poultry feed large white grains are preferred. For poultry feed grain farmers in England frequently obtain considerably more per hectare by cultivating the variety Rivet (*T. turgidum*), with very poor bread-baking qualities, than by cultivating high quality varieties.

[84] HOFFMAN and GÄRTNER. Physico-chemical studies of protein. Colloid-Symposium. Monograph. 1925.

quently conflict with one another, particularly under the conditions of inertia of capitalistic agriculture; thus, in Western Europe, for example in England and Germany, under moist-climate conditions where there is a long vegetative period, mealy wheat as a rule is distinguished by its high productivity. It is particularly favored for its enzyme action. The milling and the baking industry prefers to have vitreous grain without consideration for the interests of agriculture. In this conflict of interests of industry and agriculture, the breeders of western Europe must take a middle course.

The socialistic agriculture of our region presents new and important requirements in the cultivation of wheat. We have these new problems: the creation of an important wheat basis in the north, the extension of wheat eastward, a considerable increase in spring wheat to occupy new territories, the creation of an extensive irrigated wheat culture in the Trans-Volga region, and a broadening of the ecotypes of Soviet wheat.

The planned governmental changes in varieties present high requirements in variety standards; for the diverse and mixed varieties there must be substituted uniform standards for the different regions. The mechanization and expansion of agriculture require new variety types. The growing requirements of our own markets present the breeders with an important problem. In the shortest possible time the breeders must produce, for different regions and localities, assortments with maximum suitability.

Basic Requirements for a Wheat Variety:—

1. *High yield* under the given environmental conditions (region, locality).
2. *Constancy* of variety with little tendency to cross pollination or mutation.
3. *Quality of grain:* high flour yield, good milling, vitreousness.
4. *Quality of flour and bread:* flour of good structure, high bread volume, bread with uniform porosity, flour with high baking qualities, small salt content, good colored bread.
5. *Grain form* approaching spherical, grain smooth, without a deep crease. Embryo easily removed, not large.
6. High absolute weight of grain.
7. Color of grain in relation to requirements.
8. Chemical composition of grain, high percent of protein, high quality of gluten.
9. *Non-shattering* grain.
10. Easy milling.
11. Heads with high grain production, ideally square in cross section, with a large number of fertile spikelets and numerous grains in the spikelets.
12. *Awnless heads.*
13. Heads not breaking or falling over at maturity.
14. Grain ripening rapidly.
15. Grain not germinating in the sheath or stack.
16. *Stiff straw,* not lodging, resistant to wind and rain.
17. Optimal ratio between grain and straw.
18. Height of straw suitable for mechanical harvesting.
19. Straw of good feeding quality.
20. *Straight stems* ripening at the same time.
21. *Ecologically plastic varieties* with adaptation to wide areas.
22. *Resistance to soil and atmospheric drought.*
23. *Resistance to excessive soil and atmospheric moisture.*
24. *Resistance to low temperatures.*
25. Resistance to damaging effects of fogs (in mountain regions).
26. *Winter resistance* (for winter varieties).
27. For winter wheat good regenerative ability in the spring after unfavorable winters.
28. *Freeze resistance,* resistance to sudden changes in temperatures and thawing, to crusted soil, to soil saturation and steaming.
29. *Resistance* to stem rust.
30. *Resistance* to leaf rust.
31. *Resistance* to stripe rust.
32. *Resistance* to loose smut.

33. *Resistance* to stinking smut.
34. *Resistance* to powdery mildew.
35. *Resistance* to fusariose.
36. *Resistance* to white spot (*Septoria*).
37. *Resistance* to Hessian fly.
38. *Resistance* to Swedish fly.
39. *Resistance* to spring fly.
40. *Resistance* to green-eyed fly.
41. *Resistance* to leaf beetle (*Lema melanopus*).
42. *Optimal vegetative period.*
43. *Optimal reaction to temperature and light conditions of a given region.*
44. *Yielding ability in unfavorable years.*
45. *Suitability to agricultural conditions* (response to irrigation, to fertilization, adaptability to varied conditions, etc.) ; maximal use of fertilization for increasing seed production.
46. Presence in the variety of sufficiently distinct morphological characters to permit its being distinguished from other varieties (including chemical reactions of the grain).

The ideal wheat naturally varies in different regions, but all must have certain general characteristics. In the preceding table we have listed important properties which, so far as we know today, characterize the more or less ideal variety. This ideal is not a stable one for all times and peoples. It corresponds to our present-day requirements and present level of knowledge. It is probable that in the near future it will be changed in important ways. The wide extension of vernalization and new chemical and mechanical methods and requirements no doubt will lead to important changes in the requirements of wheat varieties. It is also evident that to combine in one variety of wheat all the best qualities with their maximal expression is as difficult as to create a domestic animal which is suited for all purposes. It is necessary to create a number of varieties corresponding to different conditions.

Proceeding toward our ideal, with these reservations, we begin first of all with high yields. Yields are due to both environment and genotype, and to a great extent are determined by the conditions of culture and those of the region. Under favorable conditions of field culture, using the best agrotechniques and fertilization, wheat can give extremely high yields. The maximal yield, so far as we know, has been obtained under the agricultural conditions for growing English wheat (*T. turgidum*) which has produced up to 52 bushels per acre (under the conditions of England). In some of the leading collective farms of the Leningrad Province and Kazakstan (near Alma-Ati) the yields in 1934 reached 30 bushels per acre. The average yield of wheat in Holland in recent years (1926-1930) thanks to a highly developed agrotechnique and fertilization, has been 22 bushels per acre, in Belgium 19.2 bushels, in Denmark 20.6 bushels, and in Germany 15 bushels.

There is a marked contrast in the average yield in different regions over a period of years, for example, 5.2 bushels per acre for Australia with well developed agriculture and 22 bushels for Holland, which is due primarily to differences in conditions: the amount of precipitation, its distribution through the months, the length of the vegetative period, temperature factors, development of diseases, use of fertilizer, etc.

So far as possible, varieties which are developed must be constant, without inclination to natural hybridization or mutation, having grain that is as nearly spherical as possible, with a high flour output. The grain must be well adapted to milling, and as vitreous as possible. The flour must be distinguished by high quality and high bread yield. The bread itself must be of good nutritive quality and porosity, with white color and attractive taste. On the world market at the present time the color of the grain, has great importance, since

this is associated with many qualities. For the most part, the world market requires red-grained wheat. It has been shown by recent French investigations of the Versailles Agronomic Institute, carried out on a large assortment of wheats, that white-seeded varieties have a tendency to be particularly inclined to germinate in the stack. This fault has particular significance in northern regions. In southern regions frequently the white-grained hard and winter soft wheats are preferred as producing whiter flour.

At the present time in the United States and in Canada, wheat is valued according to its percentage of protein.

Mechanical agriculture requires varieties which are non-shattering and yet can be easily threshed. The heads must be awnless and as productive as possible from the standpoint of the number of grains per head and the number of spikelets. The straw must be stiff and resistant to wind and rain. In a number of regions the feeding value of the wheat straw has significance. The stems must be straight.

Varieties must be plastic, so far as possible, particularly under the conditions of our varying continental climate. In general, so far as possible, varieties must be adapted to wide areas and not too narrowly specialized.

In the ideal wheat there must be resistance to unfavorable conditions of the environment, including soil, atmosphere, drought, excessive soil and air moisture, and low temperatures, and at the same time it must be resistant to fungus diseases and to a number of injurious insects.

In winter wheat there is a requirement of winter-resistance, including freeze-resistance, resistance to sharply fluctuating temperatures, to thawing, to crusting of the soil, and to soaking and steaming of the soil. The variety must have good regenerative ability in overwintering. It must make maximal use of warmth and light in the given region, *i.e.*, it requires an optimal vegetative period.

The variety must be adapted to the conditions of agriculture of a given region, must conform to agrotechnical practices and respond well to fertilization, irrigation, and mechanization. Finally, there is much significance, under our conditions where numerous varieties are used over a wide area, in the presence of features which distinguish one variety from other varieties. This characteristic has great significance in western Europe. For this purpose recently there have been used chemical methods for distinguishing grain varieties, particularly by using reactions to phenol and to solutions of caustic potash dissolved in alcohol.

We are dealing only with those properties which must be major considerations of the breeder.

In our region, governmental variety testing is the objective arbiter and also the public court passing on the quality of improved varieties, giving a guarantee of just, impartial evaluation.

* * * * *

We will look over the best of the bred varieties that are officially recognized and at present are widely distributed.

The following table gives the results of extensive collective works carried out by the governmental variety testing network during the past decade, and shows clearly, along with significant accomplishments, how much work still lies before the Soviet breeder.

The Soviet improved varieties, on the whole, are characterized by high quality grain in the regions of their distribution. Some of the varieties, such as "Caesium 0111," "Erythrospermum 0841," and "Novinka" of the spring wheats, and also a number of the winter varieties, such as "Ukrainka," "Novo-

Characteristics of Bred Varieties of Winter Wheat Recommended in SSSR:—

(for different regions)

According to a 4-value scale (4—best, 1—poorest)[1]

Name of Variety	Winter resistance	Drought resistance	Productivity	Grain quality	Flour output in %	Volume of bread loaf	Shattering	Lodging	Resistance against: Leaf rust	Stem rust	Loose smut	Bunt	Region of cultivation of the variety
1. Ukrainka, Mironovsk Station	3	3	4	4+	4—	4	3	2+	2	2	2+	1	Most regions of Ukraine and North Caucasus; the most widely distributed variety
2. Cooperatorka, Odessa Station	2	4	4	4+	4	4	3—	(2)	2	2+	3	3—	Southern part of Crimea, very dry steppes of North Caucasus, Daghestan, Azerbaidzhan, and Georgia
3. Stepnyachka, Odessa Station	3—	4	4	4—	4	3+	4—	2—	2	3+	2—	3+	Semi-arid steppes of North Caucasus
4. Novokrimka 0102, Krimsk Station	2	4	3+	4	4	4—	2+	2	(1)	3	1	2+	Northern dry part of Crimea
5. Zarya, Nemerchansk Station	(2)	2+	4	3+	4—	2	3—	3	4—	(2—)	3—	2+	Birch forest steppes and strips of Ukraine
6. Erythrospermum 0328, Stavropolsk Station ..	2	2+	4	4—	4	3	3—	4—	3	2	2—	3—	Well-watered regions of North Caucasus
7. Apulicum 77-2, Gandzhinsk Station	(1)	3+	4	4	4	1	4	2+	2—	3	(4)	4—	Azerbaidzhan and Georgia
8. Lutescens 01060/10, Saratov Station	4—	3	2+	3—	4—	3+	3	2+	2	(2+)	2—	2	Lower and Central Volga, Kursk, and Voronezh regions
9. Lutescens 0329, Saratov Station	4	3—	2	2	4—	4—	3	3	2	.	2	2	Lower and Central Volga, Kursk, and Voronezh regions

Characteristics of Bred Varieties of Winter Wheat Recommended in SSSR:—

(for different regions)

According to a 4-value scale (4—best, 1—poorest)[1]

Name of Variety	Drought resistance	Earliness	Productivity	Grain quality	Flour output in %	Volume of bread loaf	Shattering	Lodging	Resistance against: Leaf rust	Stem rust	Loose smut	Bunt	Region of cultivation of the variety
10. Hostianum 0237, Saratov Station	3+	4—	4—	3	4—	4—	3—	3—	2	2	3	2+	Ukraine, Kursk, and Voronezh regions and northern part of North Caucasus
11. Erythrospermum 07201, Bezenchuksk Station .	3+	3	3—	4—	4--	3+	3—	..	2	..	2	2	Kuibishevsk region
12. Erythrospermum 0917, Kharkov Station	3+	2+	3+	4—	4—	3	3+	4—	2—	..	3+	3—	Kursk region, southern Moskva region, and Vashir SSR
13. Ferrugineum 02411, Moskva Station	4—	2—	4—	4—	3—	3	4—	3—	1	3	4—	3	Leningrad, West, Moskva, and Ivanovsk regions and White Russian SSR
14. Ferrugineum 02453, Moskva Station	3+	2	4—	4—	3+	4	3	3	2	..	2	2	White Russian SSR
15. Durable, Ivanovsk Station	4—	2	3	4—	3+	2	3+	4—	2	1	2+	2—	All of the non-chernozem soil strip of the European part of SSSR
16. Ferrugineum 01239, Kharkov Station	4—	2+	4—	4—	4	4	3+	4	2	..	..	..	Birch forest strip of Ukraine and the Don Basin

[1] Prepared from data of the Master Testing Network In parenthesis are indicated characteristics which do not have great significance for the area of the given variety.

Characteristics of Bred Varieties of Spring Wheat Recommended in SSSR:—

(for different regions)

According to a 4-value scale (4—best, 1—poorest)[1]

Name of Variety	Drought resistance	Earliness	Productivity	Grain quality	Flour output in %	Volume of bread loaf	Shattering	Lodging	Resistance against: Leaf rust	Stem rust	Loose smut	Bunt	Region of cultivation of the variety
1. Erythrospermum 0341, Saratov Station	4—	3	3	4	4	4	3	3	1	3—	3+	1	Steppes of the Lower Volga, Kazakstan, and North Caucasus
2. Erythrospermum 0841, Krasnokutsk Station ..	4	3+	3	4—	4	4	4—	(2)	(1)	2	3	3—	Steppes of the Lower Volga, Kazakstan, North Caucasus, and Central Asia
3. Sarrubra, Saratov Station	4—	3	3	4	4	4	3-r	3	(1)	3	1	3	Saratov Region
4. Lutescens 062, Saratov Station	4—	3	4	3	3	3	2	3	2+	3	1	3—	Ukraine, Vashir SSR, Tatar SSR, Sverdlovsk, Ob. Irtish, Central Volga, Gorkovsk Region, Voronezh and Kursk Region, North Caucasus, and Daghestan SSR
5. Graecum 0289, Krasnovodopadsk Station ...	4	3+	2+	3+	4	4	4	3	(2—)	3	2	2	Extremely dry steppes of Kazakstan and Central Asia
6. Caesium 0111, West Siberian Station	3	3	4—	4	4	4	3	3	3	3	3	2	West Siberia, Trans-Ural, black earth steppes of Kazakstan, Vashir SSR, Tatar SSR, Gorkovsk Region, Kursk and Voronezh regions
7. Milturum 0321, West Siberian Station	3	1	4	3—	3	2	3	3	2	3—	3+	3	Southern forested steppes and steppes of West Siberia, Trans-Ural, and Kazakstan
8. Leda, Krasnoyarsk Station	2	3	4—	3+	3	4	3	2	3—	..	1	3+	Forest steppes of East Siberia
9. Marquis (Canada)	2	2	3	3	3	4	3	4	4—	2+	3—	3+	Moist zone of North Caucasus

Characteristics of Bred Varieties of Spring Wheat Recommended in SSSR:—
(for different regions)
According to a 4-value scale (4—best, 1—poorest)[1]

Name of Variety	Winter resistance	Drought resistance	Productivity	Grain quality	Flour output in %	Volume of bread loaf	Shattering	Lodging	Resistance against: Leaf rust	Stem rust	Loose smut	Bunt	Region of cultivation of the variety
10. Strube (Germany)	(1)	2—	3	3	3	3	(2)	4	2—	3+	1	2	Foothill regions of Daghestan SSR
11. Novinka, Detski Village Station	(1)	4—	3+	4	4	4—	(2)	3	2—	3	3	2+	Leningrad region and northern region
12. Garnet (Canada)	(2)	4—	4—	4—	3	3—	(2)	4—	3+	3—	3	3	Northern region, northern part of Gorkovsk region, Ivanovsk Region, and Daghestan SSR
13. Tulun 81/4, Tulun Station	3—	4—	3+	2	3	2	(2)	3	2	..	2	2	Forested strip of Pri-Baikal
14. Hordeiforme 0432, Saratov Station	4—	3—	4—	4	3	4	4	3	4	3—	3+	3+	Lower Volga, Kazakstan steppes, and Vashir SSR
15. Hordeiforme 0189, Krasnokutsk Station	4—	3—	3	4	3	3	4	3	4	2+	3+	3+	Central Volga, Abkhazian SSR, German-Volga SSR, Kazakstan
16. Melanopus 069, Krasnokutsk Station	4—	3	3	4—	3	3—	4	3	4	3—	3+	3—	Ukraine, North Caucasus steppes, Central Volga, Abkhazian SSR, German Volga SSR, and Kazakstan
17. Hordeiforme 010, Dnepropetrovsk Station	3—	2	4—	3+	3	3—	4	3	4	2+	4—	3	Forest Steppes of western Siberia, Trans-Ural, Vashir SSR, Voronezh region, North Caucasus zone of minimal to adequate moisture
18. Hordeiforme 027. "Kruglik" Exp. Station	3—	2	4—	3+	3	3—	4	3	4	2	3	4—	Sufficiently moist zone of North Caucasus

[1] Prepared from data of the Master Testing Network. In parentheses are indicated characteristics which do not have great significance for the area of the given variety.

krimka," and "Cooperatorka," are characterized by very high quality grain. Their tendency to shattering is another matter. Although our varieties in the past have been entirely suitable for harvesting by sickle and binder, the widespread introduction of combines requires basic revision of wheat types for developing resistance to shattering. Particular interest attaches to the standard Argentine varieties which have been created in recent years in connection with the extensive use of combines in Argentina, based upon the non-shattering character of Chinese wheats.

A great deal of work must still be done in relation to resistance to rust and particularly to smut. Even though the rust factor has rather limited significance in our dry regions, this is not at all the case with smut. The majority of wheats of both winter and spring types must be fundamentally corrected to increase their resistance to both loose and covered smut. A leading problem of breeding under the moist conditions of North Caucasus and the northern regions of the European part of the Union and the Far East appears to be breeding for immunity from leaf and stem rust.

On the whole the Soviet varieties of winter wheat are characterized by high winter resistance, surpassing other varieties of our region in this respect. The best of the winter-resistant varieties of USA have been borrowed from Crimea and Ukraine. The most winter-resistant Swedish and German wheat varieties are killed out under our conditions even in an average year. The rigorous conditions of our winters require further work on winter resistance. Only one wheat among our standards, "Lutescens 0329" developed by the Saratov Station, has entirely satisfactory winter resistance. All of the others are only moderately resistant. Under the severe conditions of our winters, for example in the unfavorable winters of 1927 and 1928, seven million hectares of wheat were killed out in North Caucasus and the Ukrainian steppes.

All the same, with regard to winter resistance and drought resistance, our wheats occupy first place in comparison with the majority of foreign standard wheats. The harsh winter conditions of the Lower Volga Region, the steppe region of Ukraine, and North Caucasus have resulted in comparatively resistant forms, but considerable work must still be done on this, and no doubt there are varieties superior to ours in winter hardiness among the Mediterranean wheats, particularly those of Palestine and Syria and also some of the Central Asiatic forms.

Although the general assortment of Soviet wheats is comparatively satisfactory in productivity, those which are most interesting from the standpoint of winter resistance, as Lutescens 0329 and Lutescens 1060 of the winter wheats and the drought-resistant Graecum 0289 of the spring wheats, have rather low productivity; moreover 0329 also has rather low grain quality.

The accompanying tables show that much needs to be done by breeders, even for those wheats which, throughout the world, are known as most winter-resistant, most drought-resistant, and highest in quality.

Of all the world standards of wheat during the past 20 years, the Canadian variety "Marquis" at present occupies the greatest territory in Canada and in northern USA. For the conditions of Canada this variety approaches the ideal in the sense of sufficient resistance to drought, rust, and smut, its high productivity, non-lodging straw, and almost completely efficient use of the short vegetative period of Canada. This variety also has grain of excellent quality and high milling and baking properties.

Unfortunately this world champion, which was introduced into Russia in 1922 in great quantity and tested on a large scale, and also studied in the Master Testing Network, showed little suitability to our conditions and may

only be cultivated with some degree of success in the sufficiently moist zone of North Caucasus.

In approaching the problem of wheat breeding we must remember that in dealing with this plant the breeder is working within much narrower confines than in working with other plants. Wheat has no great amplitude of heritable variations, being much more uniform than other plants, particularly in a number of physiological characters. For example, in size and weight of grain, wheat varieties vary approximately within the limits of 3, or a maximum of 4 times, while in other plants, even in corn, we have considerably more heritable amplitude, not to mention fruits, cucurbits, and root crops where varietal differences in important organs are expressed in hundreds and even thousands of times. In winter-resistance and drought-resistance the amplitude of variation of our varieties and species is comparatively limited, and in this respect a number of our standard varieties occupy first place. A large number of varieties of barley (including winter forms that have been vernalized) regularly ripen even within the Arctic Circle (Khibin). Of the great world assortment of spring and winter wheats, only a few varieties can ripen in favorable years within the Arctic Circle. The difference between barley and wheat, in this respect, is quite striking.

Finally, by crossing, by combining complexes of genes of different species, and different geographic races, we may considerably broaden the amplitude of variation, but still the frame of heritable variation in wheat is somewhat narrower than in a number of other cultivated plants, as we have convinced ourselves by cyclic crossings carried out on a broad scale at the Institute of Plant Industry, using the most diverse species and geographic races. In this respect breeding of other crops, for example fruits such as apples and pears, where there is a great amplitude of variation in cold-resistance, productivity, and size of fruit, may give significantly more effective results than work with wheat.

Nevertheless, the specific and varietal amplitude of wheat for practical purposes is sufficiently wide, as may be judged by the present-day geographic area of wheat culture and the contrasts which it presents. This is seen, for example, in the Siberian spring wheats with small heads and small grain, and the English wheats with gigantic heads and high productivity. *The most difficult and complex problem in breeding wheats is the necessity of combining in one variety a majority of valuable characters.* In order to approach the ideal wheat varieties, we must have the persistent combined work of breeders with physiologists, phytopathologists, entomologists, and technologists.

We now pass to a consideration of the important characters that mark the direction of wheat breeding, and first of all that of yield.

Breeding for Yield:— The English breeder, ENGLEDOW, with his co-workers, has attempted to evolve a theory of wheat yields from the point of view of breeding. The yield of wheats is determined by the production of grain per hectare and is the final result of all the bio-physico-chemical processes during the course of the whole life of the plant in relation to external conditions. The analytical study of varietal yields, in ENGLEDOW's opinion, must first of all be associated with investigations of the development of the plant, *i.e.*, it requires periodic observations during the course of the whole vegetative period. The basic factors determining varietal differences in wheat yield, according to ENGLEDOW, are principally features of the root system, differences in tillering, length of vegetative period, dynamics of growth of the plant, and accumulation of dry matter, together with varietal differences in resistance to different diseases and to low temperatures and drought. Under the conditions

of a moist climate, much attention must be directed toward non-lodging in the varieties. Each of these factors, in ENGLEDOW's opinion, if it is properly considered by the breeder, guarantees a certain number of bushels. The breeder must be familiar with his varieties from the moment of germination and the beginning of activity of the different factors that contribute to yield.

In a number of publications in the "Journal of Agricultural Science" (1924-1929), ENGLEDOW has made a detailed survey of the different factors which govern yield, namely: tillering, photosynthetic area, time of blossoming and time of ripening, weight of grain, ratio of straw to grain, influence of different diseases, and fertilization.

Direct experimentation has shown that under the mild humid climate of England a number of varieties of squareheads and a form of *T. turgidum* (Rivet) are quite distinct in their potentiality for giving high yields. Under the conditions of England, as well as in some other coastal areas, these two groups of wheat must be rated as highest in productivity.

Varietal differences in yield are no doubt very great, but investigation of these differences necessarily must be related to the environment. The maximum yields for different varieties will occur under different conditions. For example some varieties show a marked increase in yield when they are fertilized, while others are comparatively unresponsive to fertilization.

The investigation of varietal differences in yields, particularly in those cases when the differences are not great, requires very uniform testing conditions, replicated plots, and repetition of the experiments over a series of years. An extensive literature is devoted to the methods of variety testing for yields.

The relationship between yield and the several components that contribute to it has been the theme of investigations on a number of different occasions. In "The Law of Yields" A. A. SAPEHIN (1922) reported his determination of the relationship between yields and density of plant stands. In all cases the factors determining yield in wheat are so numerous and so interwoven with environmental conditions and reciprocal relationships, that to resolve them into an integral theory of variety yields is very difficult, the more so since at the present time we are faced with the problem of working over the agrotechniques of varieties (density and time of sowing, etc.), specifically for the different varieties, and these differences may vary markedly in extreme variants. In the brief characterization of the "ideal wheat" given above, an attempt was made to embrace the various properties determining size and quality of yield under different conditions. In any case, under a given set of conditions varieties show considerable difference in productivity with a range of variation of severalfold. As an example of extreme variation we have the high-yielding English squareheads and the southern European forms of *T. turgidum* which give maximal yields under temperate-warm moist climatic conditions, and, on the other hand, early maturing, low-growing, few-tillered emmers and hard wheats of Arabia, with low productivity even under optimal conditions for their culture. Such a factor as the infection of some varieties with disease when others are unaffected gives even more striking contrast in the yields of varieties.

Breeding for Immunity from Diseases:— The number of diseases affecting wheat is quite considerable: three species of rust—stem (*Puccinia graminis*), leaf (*P. triticina*), and stripe (*P. glumarum*), loose smut (*Ustilago tritici*), and bunt (*Tilletia tritici* and *T. levis*). In China the leaf smut (*Urocystis tritici*) is widely distributed. In addition wheat suffers from fusariose, leaf spot (*Helminthosporium* and *Septoria*), and powdery mildew (*Erysiphe graminis*). Usually wheat is attacked by Swedish, Hessian, and other flies.

Such is the long list of very important pests of wheat. With respect to all these diseases and insect pests, as is well known at present, there are varietal differences in resistance.

The difficulties in breeding include the fact that each of the numerous parasites, particularly species of rust and smut, occurs in the form of many races which behave differently with respect to a given variety. Although with some diseases we may practically disregard physiologic races, in relation to stem, leaf, and stripe rust, and also to bunt and loose smut, the question of races has great significance and we cannot disregard them in breeding work.

At the present time there have been described more than 50 races of leaf rust of wheat, more than 150 races of stem rust, 14 races of stripe rust, no less than 8 races of bunt, and at least 5 races of loose smut.[85]

The significance of races of parasitic fungi in the case of rust may be judged from an example taken from Römer (1934). In 1911 in Germany the Swedish variety of wheat "Panzer" of the Svalöf Station was widely grown, and because of its high yield it soon occupied a great area. This variety at first was considered to be resistant to stripe rust, and actually it was not attacked. Races of stripe rust to which this variety was susceptible occurred only in very small quantity, since in Germany the varieties grown extensively were not attacked by such races. As the area of cultivation of the variety Panzer increased, there was created a more and more favorable situation for the development of the races of stripe rust which could attack it, and finally in 1923 the development of these races of rust became so extensive on the variety Panzer that this variety was liquidated.

Römer has given a similar example for loose smut. On one of the old varieties of wheat, "Grüne Dame" produced by Woltman there was found a distinct physiologic race of loose smut. Since this variety was rather rare in Germany the occurrence of this race of loose smut, until lately, has had no practical significance. During recent years the breeding stations introduced into culture new wheat varieties which were very productive and valuable in many respects, but susceptible to this particular race of loose smut which occurred on "Grüne Dame." As a result, this formerly rare race of loose smut has become widespread in Germany. Unfortunately the question of physiologic races of fungi in SSSR has been studied very little with the exception of a few local works (in Odessa and in Omsk).

The study of the immunity of wheat until recently had not been well worked upon, since private breeding, up to this time, prevailed in Western Europe and facilities were not available for special scientific investigations of the etiology of parasites or serious studies on physiologic races of fungi. It was only with the creation of governmental breeding and phytopathological institutes and experiment stations in the past decade that this question began to be studied. We should give particular attention to the work of phytopathologists and breeders in U.S.A., Canada, Germany, Sweden, England, and Australia.

An important fact having decisive significance in breeding for immunity is that many species and varieties of wheat may combine immunity from different diseases and also from many physiologic races within the limits of a single parasitic species. *Group immunity,* which we demonstrated in 1913-1919, is widely distributed among varieties and species of wheat with respect to leaf, stripe, and stem rust, and also from loose and covered smut and powdery mildew, which greatly facilitates breeding for immunity. This fact must be regarded as basic in the breeding for resistance to diseases.

Moreover, in the distribution of immunity among species and varieties of

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[85] N. Vavilov. [Immunity of plants from infectious diseases.] Leningrad, 1935.

wheat there are observed definite regularities: certain species, particularly among the group of 28-chromosome wheats, are characterized by the widespread occurrence of group immunity. A number of ecological-geographic groups, for example emmers, are distinguished by striking immunity at one time to several species of fungus pathogens, including whole complexes of physiologic races which comprise them.

Our investigations carried out on the great world assortment of wheats definitely showed the wide distribution of group immunity in connection with the genetic differentiation of wheat species. The most distantly related species, such as einkorns and timopheevi wheat, were characterized by the highest expression of immunity from almost all infectious diseases. The "Persian" wheat (*T. persicum*) which we separated out in 1919 and which has immunity from powdery mildew and rust, later was found to be exceptional genetically and cytologically, in its number of chromosomes. The genetic investigations (N. Vavilov and O. Yakushkina, 1925) fully confirmed the distinct position of this species in the wheat system. Within the limits of given species, differentiation into ecological-geographical groups is parallel to marked differences in immunity reactions, for example in hard wheat, emmers, and *T. turgidum.* Western European and western Mediterranean subspecies of these species are distinguished by their immunity from leaf, stem, and stripe rusts and powdery mildew; the Abyssinian subspecies are comparatively susceptible. Whole regions of ancient culture of wheat are characterized by a concentration of immune varieties and species. In this connection Trans-Caucasus, Armenia, Georgia, and the Karabakh foothills have particular interest to us, since here are concentrated the species that are most noteworthy for immunity, such as *T. timopheevi, T. monococcum,* and *T. persicum,* the latter with a large diversity of varieties.

The present-day Soviet standard assortment, as we have seen, in the case of soft wheats is far from ideal as regards resistance to leaf and stem rust. The variety standards of the U.S.A. and Western Europe, which are particularly adapted to local conditions, are distinguished by a greater expression of immunity, the result of special breeding in this direction. Unfortunately for us, the results of this breeding for rust resistance do not have great significance, since the breeding work was directed at those species of rust which are least widespread in Russia (*Puccinia glumarum* and *P. graminis*), not to mention the different physiologic races. The situation is somewhat better with respect to smuts, but even here we must consider the possibility of the presence in Russia of distinct races of the smuts. The nearness of the Soviet Union to the region of origin of cultivated wheat species, and consequently to the place of origin of forms of many parasitic fungi, suggests that we will find in our region a great diversity of physiologic races.

Recent investigations on smuts and rusts of cereals have shown that we have not only a diversity of races, but evidently species of fungi which are peculiar to Central Asia and Trans-Caucasus.

Before leaving the subject of genetics of immunity of wheat from parasitic fungi, it is very essential to point out the demonstration in wheat of the difference in behavior of seedlings, with which the phytopathologists usually work in artificial inoculation experiments, and of older plants in the field, which is paramount for practical breeding.

Not all varieties which are susceptible in the greenhouse in the seedling stage are attacked in the field.

In "Studies on Plant Immunity" (1935) we have outlined in detail the

level of present-day knowledge of the genetics of immunity of cereals, particularly wheat.

The investigations definitely show the Mendelian behavior of wheat immunity, the possibility of combining it with other valuable characters, and the usual dependence of immunity on several hereditary factors.

Resistance of wheat varieties is seen not only with respect to parasitic fungi, which are narrowly specialized, but also to such insects as the Hessian and Swedish flies. For example PARKER, PAINTER, and SALMON in the U.S.A., as a result of testing 400 winter wheat varieties, found 14 varieties which were comparatively resistant to the Hessian fly. Among these were such varieties as "Malakoff," "Michigan," and "Red Rock." In this work there was found an interesting rule: the resistant varieties were particularly wheats with highly mealy grain. Only one variety, "Fulcaster," was an exception. When its genealogy was analyzed, it was found that it had been derived from an old variety with mealy grain. In contrast, forms with vitreous grain were attached most strongly. A number of investigations on resistance of wheat to different species of flies have been carried out by us in the Shatilov and Saratov Stations.

Work in the Odessa Breeding-Genetics Institute has shown the possibility of creating forms of wheat with resistance to the Hessian fly, by appropriate combinations of varieties differing in developmental stages.

Breeding for Chemical Composition:— It is becoming necessary for the present-day breeder to give more and more attention to the chemical composition of wheat. In the U.S.A. the evaluation of wheat grain includes, as a regular requirement, determination of the protein percent, which is designated on the sack and in all cases is required on large consignments. Every carload of wheat is marked with its protein content.

A decisive role in determining the percentage of protein is played by environment, climate, and soil conditions; moreover, as we know from our geographic experiments and from our data on variety testing, the quantity of protein in wheat follows definite geographic rules: under the conditions of the European part of SSSR the production of protein increases as we go southward and to the drier regions, while it becomes lower to the west and then rises again in the extreme north.

According to the data of our organized geographic experiments with many varieties and species of spring wheat, in protein analyses for four years in the Biochemical Laboratories of the All-Union Institute of Plant Industry (N. N. IVANOV) the average percent of protein was as follows, according to regions:

REGIONS:—	
North	11.8
Northwest	14.3
West	14.6
Northeast	15.3
Central	16.7
Ukraine	18.5
Crimea	14.6
North Caucasus	17.3

REGIONS:—	
S. E. European part of SSSR	18.9
Western Siberia	18.5
Eastern Siberia	18.3
CENTRAL ASIA:—	
Irrigated spring sowings (Tashkent)	16.5
Non-irrigated spring sowings	19.4
Winter sowings	12.7

A single variety varies sharply in relation to conditions. For example, one of the varieties of hard Abyssinian wheat contained only 10% protein in the original grain which we gathered in Addis Ababa, while in Persianovka near Novocherkassk it produced 20% protein. The variation from year to year in a given variety at these points was considerable. According to the data of the Governmental Testing Network, in the southeastern European part of

SSSR the range of variation of averages for a number of varieties in different years was from 14.1 to 21.2% and in western Siberia from 15.33 to 18.2%.

In an interesting report on analyses of original wheat samples, prepared by K. A. Flaksberger (1932) from data of the Biochemical Laboratories of the All-Union Institute of Plant Industry, there are given the protein percentages for wheats of all regions of the world.

Low percentages of protein occur in regions with irrigated agriculture, such as Egypt (average 9.7%), western China (11.3%), and well-watered regions in the mountains of Tadzhikistan (10.3%). A low protein percent was characteristic of the moist region of Abyssinia (11.3%). The Mediterranean region, where wheat is sown in the fall, despite the predominance of hard wheat does not show high protein content (Sicily, 12.2%; Sardinia, 13.3%; Syria, 13.1%; Palestine, 14.1%; Tunis, 12.7%; Morocco, 14.0%; Algeria, 14.1%).

Argentina and Uruguay are characterized by an average of about 13.32%. Australia shows much variation, from 8.4-18%. Canada, where spring wheat is primarily grown (in 11,000,000 hectares of wheat, not over 300,000 hectares are winter wheat), is characterized by a high quantity of protein (about 16.5-17%).

Rumania (11.2-15.6%), Hungary (10.9-13.5%), and Yugoslavia (12.9-15.0%) produce wheat with only moderate protein content, which evidently is associated with winter wheat culture which, as a rule does not favor high protein percentages. The average protein content for SSSR, is approximately 16%, according to data from the geographic experiments, the Master Network, and in the literature.

In SSSR the highest protein percent is found in spring wheats of the southeastern European part (18-19%), the steppe region of Caucasus (16.5-18.5%) and western Siberia (16.3-18.4%). In extreme years the protein in these regions in certain varieties may go as high as 24.6%. The high average figures for Russia are due to the predominance of spring wheat (25 million hectares compared with 11 million for winter wheat), and the dryness of our climate where spring wheats are principally cultivated. A high percent of protein also characterizes spring wheat in U.S.A., viz., in Montana (17%), in North Dakota (18%), and winter wheat in the dry states of Kansas (17%) and Nebraska (18%).

The greatest concentration of high protein wheat in the world is in SSSR, namely in the southeast European part, Kazakstan, and the steppes of western Siberia. The second largest concentration is in the prairie region of America. The highest protein percentages occur in chernozem and chestnut soils, where there is a dry continental climate, and where agriculture consists chiefly of spring wheat cultivation.

Irrigation usually lowers the percent of protein. In general the reduction, due to irrigation as shown by data from America and Canada, is 1.5-2%, but this depends on the time and quantity of irrigation, and if sufficient attention is given to management of water supply the protein percent may hardly be lowered.

The percent of protein in wheat grain varies, in relation to environmental conditions, from 7 to 24% on the basis of air-dry grain weight. The amplitude of varietal differences is not as great as extreme variants (seen in unusual conditions of growth). S. Vorobev (1927) has found 4.5% variation for the wheats of Ukraine, and Miège 4.9% for Morocco. The highest quantity of protein, according to the analyses of the Biochemical Laboratories of the All-Union Institute of Plant Industry, was 24.6%.

The conditions of our continental climate and the rather high level of soil nitrogen, as shown by extensive analyses of the Biochemical Laboratory, are responsible for the general high protein content and to some extent for a cancelling out of varietal differences: for spring wheats of SSSR approximately 16-18% in the basic regions of their culture, and for winter wheats about 12-14%. Reports from the milling-baking laboratory of the All-Union Institute of Plant Industry, indicate that irrigation in the dry conditions of the southeast European part of Russia hardly lowers the quality of grain. According to data of the Central Asiatic Section of the Institute of Plant Industry and the Biochemical Laboratory (N. N. IVANOV, M. I. KNYAGINICHEV and V. K. KOBELEV) different wheat varieties react differently to soil; in poor soil some of them show no reduction in protein, others a moderate reduction, and still others a major reduction. In breeding for irrigation agriculture, naturally it is necessary to select varieties in which the grain protein is least affected by watering.

According to the data of N. M. TULAIKOV and N. F. PISAREV (1926) varieties of wheat differ in their tempo of accumulating protein nitrogen.

As regards grain quality, the 28-chromosome group of wheats deserves particular attention, including species and forms which are particularly valuable for the colloidal and physical properties of their protein. Here belong the whole group of macaroni wheats. The complete separation of the endosperm from the seed coat is easier in hard wheats than in soft ones, and this is associated with a higher output of flour.

J. A. CLARK (1926) crossed Hard Federation × Marquis, in which the first variety has an average protein content of 13.99% and the second 14.94%, and obtained an F_1 in which the average protein percent was 14.37. In the F_2, in 567 different plants, the protein varied from 12.5 to 17%.

Under the moister northern climates the chemical individuality of varieties is more striking, but in the southeast European part of Russia, for example in the Kuibishevsk and Stalingrad regions, even hard and soft wheats in general differ little in their protein content, although in the Leningrad region (Detski Village) the same varieties varied strikingly, with differences reaching 20 to 30%. For example, while the two wheat varieties *hordeiforme* and *pseudo-hostianum* grown in Saratov had 19.5 and 19% protein, in Detski Village they had but 12 and 15.5%. Frequently variety differences in protein in the Leningrad region are considerable when they are compared over a period of years. For example, according to the data of the Biochemical Laboratory of the Institute of Plant Industry, the percent of protein in two wheat varieties at Detski Village during four years showed the following differences:

	1921	1922	1923	1924	Average
Ferrugineum 85/14	16.7	16.2	17.3	18.3	17.12
Hybrid 31	13.8	13.7	9.0	13.3	12.45

Varietal differences in the accumulation of nitrogen, as shown by the investigations of GERICKE[86] were brought out in particular relief against a background of nitrogen fertilization. Differences in the accumulation of protein in his experiments reached 25% (Australian variety Bunyip and Indian variety Pusa).

According to the data of MIÈGE in Morocco[87] varietal differences in the quality of gluten (extensibility, elasticity, tendency to deformation) vary with the use of fertilizers. Complete mineral fertilization does not increase the quality of gluten in all varieties.

[86] GERICKE, W. F. Journal of Cereal Chemistry 10. 1933.
[87] MIÈGE, EM. La valeur boulangère des blés du Maroc en 1932.

Excessive protein in the grain does not result in an improvement in bread-baking qualities. Data of the Milling-Baking Laboratory of the Institute of Plant Industry have shown that in hard and soft spring wheats there is an improvement in baking quality as protein increases up to 17-21%, and a lowering of quality with more protein.

We note significant works in recent times on the improvement of the quality of gluten in Germany and Sweden by using small amounts of bromine salts; for example 0.001% $KBrO_3$ gave positive results. This region produces particularly low quality grain, and there the question of improving the gluten is a very important one.

The determination of nitrogen by the Kjeldahl method and from it the determination of the percentage of protein, however, is only a first approximation of the differences in chemical individuality of varieties. The works of the Biochemical Laboratory of the Institute of Plant Industry (N. N. Ivanov) have shown that the flour from spring wheat has a lower proportion of gliadin to glutenin than in winter wheat. In both hard and soft spring wheats, the ratio of gliadin N to glutenin N was 0.7-0.8 and for winter wheat it was 1.1-1.2 or higher.

According to the data of Hoffman and Gaertner the albumin of wheat, gliadin, contains different quantities of the amino acids lysine and histidine in different species. *T. spelta* and *T. dicoccum* were very rich in lysine, almost 5 times more so than *T. vulgare*.

The same authors determined differences in the amino acid arginine in wheat varieties (25-30%).

The content of salt under uniform conditions, according to the data of the Biochemical Laboratory also varied sharply in different varieties, some samples having twice as much as others. Over a period of years (1930-1932), Ukrainka accumulated 12% more salts than Lutescens 1060/10. According to the literature, winter wheats contain less salt than spring wheats, and vitreous wheats more than mealy ones (N. N. Ivanov). A single variety such as Caesium 011, in the experiments of the Master Network in Rostov, yielded 2.15% salt and in Semi-Palatinsk, 1.49%.

Reactions to phenol and to caustic potash dissolved in alcohol showed great differences in the grain of different varieties. These reactions are widely used at present for distinguishing varieties. The reactions indicate chemical differences in the grain of the different varieties.

Breeding for Milling and Baking Quality:— The grain of wheat is used principally for preparing flour for different types of bread and cake, for macaroni, and, to a comparatively small extent, for heavy industry. The present-day milling industry has set up definite requirements in grain quality. The millers draw a sharp distinction between hard and soft wheats, and within the limits of soft wheats they distinguish mealy, vitreous, and semi-vitreous grains. Among the Abyssinian wheats there are original forms with waxy grain (Biffen). The shift of the milling industry to use of rolling mills has changed the requirements of grain quality. Instead of mealy grain, the world market today requires vitreous grain, rich in protein with high bread-baking quality, producing a good-sized loaf that is fairly rigid, with good porosity, and bread that is easily assimilated. All regions that export wheat grain such as Argentina, Canada, U.S.A., and India maintain first-class laboratories for studying milling and baking quality, and all of the breeding work today in these regions is concerned with the requirements of the milling industry.

In evaluating grain the following factors are usually considered: nature of

grain, weight per thousand grains, vitreousness, flour output, appearance of flour, porosity of bread, water-absorptive power of flour, color of dough, and size of loaf. The bread-baking quality is determined by different formulas which include the factors mentioned above. German investigators (ENGELKE and others) consider that high quality wheat is wheat that gives a good flour output and produces a large loaf on baking, with uniform porosity; the bread must have good qualities without necessity of supplementing the flour, and it must have normal taste and color.

The most important factors in the quality of bread are porosity and loaf volume. These two characteristics today are basic in evaluating varieties, hence we include them in our characterization of standard varieties.

For flour output the *grain form* has decisive significance. One of the great achievements of Canadian breeding is the fact that the variety "Marquis" has barrel-shaped grains, which is associated with its rather high flour output. As regards good grain form, the outstanding species are *T. sphaerococcum,* which was described by PERCIVAL, and the Syrian-Palestine hard wheats (*T. durum horanicum*) which are particularly widely grown in Trans-Jordan. These wheats deserve special attention of the breeder for crosses.

The *milling quality* of grain deserves particular attention. Vitreous wheats are milled more easily in rolling mills than are the mealy ones.

The *flour structure* or its consistency also has significance. Wheat varieties are clearly divided, according to their flour, into grainy and floury. The first type has the consistency of fine sand, the second, of dust.

Varietal differences in milling and baking qualities are very striking. For example, the volume of loaf, according to the data of the Technological Laboratory of the Institute of Plant Industry, varies according to variety from 210 to 630 cc. for a given quantity of flour, *i.e.,* threefold. The characteristic of *loaf volume* is basic in evaluating wheat varieties and the flour they produce. With it are associated fine grain of the bread and good porosity, and in general it summarizes bread-baking quality.

The high requirements of the industry have led to deeper and deeper studies on the specific differences of flours from different wheat varieties and studies of the process of aeration of the dough and evaluating dough consistency. The Milling and Baking Laboratories of Minnesota and Kansas have made detailed studies of the flours from different varieties of wheat with respect to structure and fermentation of the dough, fermentation curves, and "life of the dough."

The direct determination of milling-baking quality as carried out by us requires a large quantity of grain, no less than 1-2 kilograms, for evaluating varieties in the governmental variety tests; for breeding purposes attempts are made to bake with small quantities of flour or to use the so-called indirect or differential methods.

Most important among the differential characters in the evaluation of flour, as all authors agree, is the quality of the gluten, its extensibility, elasticity, and rigidness. This requires methods for evaluating the gluten. The VILMORIN firm in France has widely used the Chopin apparatus which determines extensibility of the gluten and its firmness. Whole assortments and different hybrid lines, beginning with the 4th generation, are tested with the Chopin apparatus. According to the reports it gives good results. The BRABENER method determines elasticity of the gluten and its stiffness by using the farinograph and gas formation with the fermentograph.

BERLINER and KOOPMAN have worked out a new colloidal method of determining gluten quality, based on solution and swelling of the gluten.

Finally PELSHENKE in Germany has developed the so-called fermentation method (Schrotgärmethode). The method of PELSHENKE is particularly interesting in the fact that it requires only a very small quantity of grain. It has 0.8 correlation with the ordinary method of analysis using a larger quantity of grain.

It is rather significant that the best agreement of the method is with the high-quality varieties; there is less agreement in the group of low quality varieties.

ROSENSTIEL (1934) worked out a method of preliminary evaluation of grain for flour quality by using probes no larger than a single gram. As shown by tests of this method in Halle, one of the best breeding-milling-baking laboratories, it gives comparatively good results.

It is necessary to note, however, that in the results of these methods there exist considerable differences, particularly in relation to the method of PELSHENKE (ENGELKE and others).

The method of PELSHENKE has recently been studied and improved in the Göttingen laboratories (ENGELKE). In modified form this method makes it possible to evaluate small probes for quantity and quality of gluten and for diastatic and proteolytic power. This method also gives an indication of firmness of the dough and character of its porosity.

BIFFEN in England first gave attention to the inheritance of flour quality in varietal crosses and the Mendelian segregation of this property, and demonstrated the practical possibility of combining high quality grain with productiveness.

Even under the conditions of England, with its very moist climate, he developed two varieties, "Yeoman I" and "Yeoman II," which combine significantly high yields with a comparatively good quality. The hybrid forms are intermediate between their parents.

In the works of PELSHENKE, in different crosses which he made, high quality gluten behaved as a recessive character, which gave the possibility of beginning selection of valuable forms in the second hybrid generation, but as a general rule high quality flour is determined by several genes which are evidently different. Moreover, as is well known, the quality of flour is closely related to the external conditions of wheat culture. For investigating the inheritance of grain quality, it is particularly necessary to use the differential and indirect methods.

The Swedish Svalöf station has recently given great attention to the genetics of flour quality and breeding for it. NILSSON-EHLE and ÅKERMAN have shown that in crossing closely related varieties of similar ecotypes, even in the 4th generation one may select out forms of wheat with high quality. In the 5th generation the problem of selecting out such varieties is usually decided. It is quite a different matter in crosses of different ecotypes, for example in crossing Swedish with Russian varieties or American varieties with Swedish ones. Segregation in these cases is rather complicated, so that to decide the question requires extended work over ten generations and a large quantity of plants.

The works of BIFFEN, the Svalöf Station, the VILMORIN firm, and that of RÖMER in Germany have shown the possibility of combining high productivity with high quality of grain by hybridization, despite the ordinary correlation of good grain quality with comparatively low yields (PERCIVAL).

In breeding for milling-baking quality in spring wheats, the 28-chromosome group deserves particular attention, since it includes very desirable species and types as respects grain form, high flour output, and quality of the flour itself.

Breeding for Vegetative Period:— A basic factor in wheat breeding is the length of the vegetative period. The extension of wheat to the north, and also the necessity of shortening the development of the wheat plant in dry southern regions to permit it to escape summer droughts, and in wet regions for escape from rust attack—all these bring out the great significance of breeding for early-maturing forms and at the same time forms that will make maximal use of the sun's energy.

The success of Canadian breeding, which has been responsible for the wide extension of this crop far to the north, is associated with breeding for early maturity. Australian and Indian breeders have been successful in recent years in developing early wheat varieties which are necessary in Australia and India in view of the short moist period.

With the vegetative period are associated many properties determining escape from freezing, from drought, from rust, and from insect attack, and it is also associated with such properties as grain quality.

The investigations of the last decade, the works of ALLARD and GARNER in America, the geographic experiments carried out by us with the same varieties over the whole territory of the Union, and particularly the noteworthy work of T. D. LISENKO, very clearly show the marked dependence of vegetative period not only on the genotype, but also on external conditions that govern the development of varieties. Forms that are early-maturing under one set of conditions may be late under another. "Marquis" is a spring variety in Canada and in Russia, but in Argentina it is regarded as a winter variety. Many varieties of wheat appear to be winter forms under the conditions of Kazakstan, but when grown farther north are of spring type. A variety of wheat cannot be designated as of winter or spring type or as late or early outside the concrete set of conditions in the region where the variety has been grown. Vernalization converts winter forms into spring forms, and late forms into early ones.

The vegetative period of a variety is determined both by its genotypic peculiarities and by the combination of external factors under which the variety develops.

The works of T. D. LISENKO have developed the theory of plant development, the basic element of which is the stage-development of plant organisms. By stages we understand the qualitative, specific changes in the growing point of the stem without which further normal development is impossible, and which guide the formation of different organs and characters up to fruiting. The vegetative period, in the light of present-day experimental data, must be regarded as the sum of time intervals necessary for the plant to pass through the various developmental stages. The rapidity through which a given stage is passed is determined both by the genotype and by the complex of environmental conditions. Each separate stage of development may be passed through only under definite environmental conditions which are peculiar to that stage of the variety, and this may occur no earlier than the completion of the previous stage.

At the present time we understand that there are two definite stages of development: the first—the temperature stage or stage of vernalization, and the second—the blossoming stage. For passing through the stages a complex of factors is necessary, *viz.:* temperature, air humidity, light, darkness, etc. In the first stage the most influential factor appears to be temperature. In this stage vernalization may affect the wheat embryo, although it is barely started into growth and the seed coat is nearly or entirely impermeable. Thus for

treating ordinary winter wheat, it is necessary to subject the plants to low temperature, from +1 to 6° C.

Soviet science of recent years, particularly the investigations of T. D. LISENKO, have altered our understanding of the vegetative period, permitting an intelligent explanation of the causes of the retardation or acceleration of the vegetative period.

The study of the first stage of development of wheat in the great world assortment, just as for other cereals, was undertaken to determine the relationship between the length of this stage and the location where the variety is commercially grown. For example, different varieties and species of wheat from the Mediterranean region have long vernalization stages requiring lower temperatures in distinction to the northern assortments. This kind of geographic relationship shows that the requirement for definite conditions of vernalization has a basic physiological character, associated with the evolution and production of the different forms.

In the second stage we must also consider, besides light, the other factors of the environmental complex, particularly temperature. Thus, wheats of Abyssinia, Cyprus and Arabia, according to the data of V. I. RAZUMOV, require, during the blossoming stage, much higher temperatures than Canadian or our northern wheats (for instance Garnet and Novinka). The heritable varietal differences in vegetative period in wheat are very marked. In growing a series of spring wheats in the field under one set of conditions, there may be observed a varietal gradient in vegetative period from 2 to 6 months and more. Some ecological-geographical groups are distinguished, under our ordinary conditions of field culture, by striking earliness, for example, Indian and Arabian forms, our northern races, Finnish and Norwegian wheats, etc. Within the limits of the great world potentials of wheat there is much opportunity for creating various types of combinations of spring and winter forms.

The types of earliness in wheat differ: one variety under given conditions grows rapidly in the first phase of its development, from tillering to heading, while another, on the contrary, goes rapidly through the last phase, from heading to ripening. Some northern forms ripen at low temperatures, for example *T. persicum,* the Abyssinian subspecies *T. durum abyssinicum,* and *T. turgidum abyssinicum;* a number of southern forms, for example all hard wheats of the Mediterranean region, require high temperatures in the later period of growth.

Along with varieties which are narrowly specialized in their vegetative period, there is a universal type of earliness, expressed in the property of rapid growth under various conditions. By crossing different ecological types, one may create the universal type of earliness, which actually has been done in the history of breeding wheat. For example, the variety "Aurora" developed by FARRER in Australia, performs very well under the conditions of northern Sweden, Finland, and with us in the Leningrad region. Evidently this is also true of some of the Argentina varieties, such as Lin Calel and others, which grew very well in the conditions of the Leningrad region in 1933-1934.

Genetically, the vegetative period is governed by a number of genes. NILSSON-EHLE advanced the view of the polymeric nature of the vegetative period in wheat.

THOMPSON (1919-1921) in Canada and FLORELL (1924) and STEPHENS (1927) in the United States investigated the genetics of the vegetative period and found that earliness was governed by a series of genes with a cumulative effect. From their data it was difficult to determine the number of heritable factors determining the vegetative period. Usually, in the crosses studied, there was transgressive inheritance in the F_3, with all gradations of earliness

within the limits of the parental forms; there were numerous cases where this went beyond the limits of the two parents.

In the older work of SPILLMAN and CHERMAK there is reference to the dominance of the winter form of life in wheat. In later investigations of wheat, on the other hand, the spring form of life was usually found to be dominant. In rice, according to the data of Japanese investigators, lateness is often dominant over earliness. In tobacco and beans there have been noted cases of dominant lateness. In wheat often the first generation is most like the earlier parent, but is somewhat later in blossoming and fruiting than the earlier parent, *i.e.,* occupies an intermediate position.[88]

In one of his experiments NILSSON-EHLE (1917), in crossing the winter wheat "Sol" with the spring wheat "Kolben," found that segregation in the F_2 followed a ratio of 3 spring to 1 winter type. Usually the F_1, in crosses of winter and spring forms, is somewhat later in maturity than the spring parent.

In a recent work (1935), T. D. LISENKO and I. I. PREZENT, in emphasizing the dominance of the spring form of life and early maturity under ordinary conditions in crosses of wheat and other plants, stated that the second and later generations of hybrids *do not and can not produce earlier maturing forms than the first generation.*[89]

Hence these authors arrived at the view that hybrids may be selected or culled for earliness directly in the first generation, considering that if the first generation is comparatively late for the given region, the same combination would not be able to give any earlier forms in later generations. This would naturally simplify the breeding work.

In general this assertion is in disagreement with ordinary genetics and breeding. Actually the experimental material on this point in the world literature is insufficient, because the first generation and the later ones are usually grown not in the same year, but in different years, and consequently under different conditions. In this connection it is necessary without delay to conduct wide investigations on the whole world assortment.

In a detailed study of our crosses of winter club wheat with early ripening wheat, under the conditions of Saratov (1919-1921), in the second and third generations there appeared plants and whole families (studied through the 4th generation) which had no tillering ability (with one stem) and were definitely much earlier than the original spring parents. The low degree of tillering (in extreme variants up to 100% of one-stemmed plants in whole families) was plainly related to the short vegetative period. The spring form of life, in this case, was dominant over the winter form (VAVILOV and KUZNETSOVA, 1921). The first generation was several days later than the spring parent.

The study of the genetics of the great world assortment of flax, which we made with E. V. ELLADI (1934-1935), led us to note many times the very definite fact of the appearance, in the 2nd generation, of forms that were considerably earlier than the first generation hybrids, under conditions in which the 2nd generation was grown alongside the plants of the first generation. For example, this was observed by us during two years in hybrids of late forms of curly flax from Abkhazia with typical flax from Afghanistan. Of 170 plants in the 2nd generation, 75 plants showed earlier blossoming than the first generation, while the most extreme forms were eight days earlier than the first generation.

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[88] Data on the vegetative period in plant hybridization are to be found in the review of plant genetics by MATSUURA (2nd ed.).

[89] T. D. LISENKO and I. I. PREZENT. [Breeding and the theory of stages of plant development.] Selkhozgiz, 1935.

In another cross of the same late Abkhazian form of flax with an earlier variety, of 397 plants of the second generation, 182 were earlier than the first generation. Many extremely early forms outstripped the first generation by five to eight days. In both cases the early habit was dominant. The first generation blossomed and ripened nearly at the same time as the early parent.

In a number of crosses of wheat in the work of the Institute of Plant Industry, there was observed in later hybrid generations, the appearance of forms that were earlier than those of the first generation. Such facts have been frequently observed by us and other investigators in crossing wheats of different chromosome numbers.

Thus we consider it indispensable, in breeding for earliness, to study the second and later generations, considering the possibility of earlier forms appearing in the process of segregation. This is all the more necessary since breeding always deals with complexes of characters, the combining of which requires study of the later hybrid generations and selection from them.

The study of growth stages leads us to a new understanding of the genetics of the vegetative period. It is clear that in choosing different physiological types as parents for crossing it is entirely possible from two late forms to obtain early ones. If, for example, we choose a variety which has prolonged growth in the first stage, with more rapid growth or normal growth in the second stage, and cross it with a variety in which the first stage is short but the second stage requires longer time, it might be possible in the progeny to obtain forms distinguished by their earliness, having inherited the short stages respectively from the two parents.

The genes determining earliness may not necessarily be identical. The facts of development by stages clearly bring out the complicated nature of the vegetative period. We must consider the relationships of genes among themselves and in reaction with the environmental conditions, hence we usually do not have an arithmetical sum of the effects of genes. From this we can understand differences in the behavior of the F_2 in segregating for vegetative period under different conditions of light and temperature.

The study of developmental stages overturns our older ideas. In order to produce new, early varieties, it is no longer necessary to aim at crossing early parents with late forms as was formerly done, but it is possible to use late parents and nevertheless obtain progeny with a significantly more rapid vegetative period in cases in which the lateness of the parents is of different nature in the two stages.

The study of growth stages shows that there is no fundamental difference between spring and winter varieties or between plants with short and long vegetative periods. Practically, under given conditions, we start out with what we consider to be winter and spring forms. We must not forget, however, that this is a concept relative to a given set of conditions.

Studying the behavior of the different stages of varieties we may foresee how they will have particular interest for obtaining desired vegetative periods for given sets of conditions. The colossal amount of varietal materials which the breeder has at his disposal today may be used systematically for selecting pairs of breeding parents to obtain desired vegetative periods, and since the vegetative period is accompanied by other characteristics, this considerably broadens the diapason of the planning of breeding work. It is quite probable that in the near future we may expect interesting practical and theoretical results along this line.

T. D. Lisenko has shown that varietal differences in growth stages follow

MENDEL's Law in heredity, giving us the possibility of deliberately selecting parental pairs for crossing and obtaining desired combinations.

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As a rule, early ripening varieties, under conditions of long and favorable vegetative periods, appear to be less productive than late-maturing varieties, which is understandable physiologically, since assimilation is restricted to a shorter period. Yet there is sufficient possibility for breeding along this line since we are not dealing with simple correlations.

The Svalöf Station has been able to combine early maturity with high yields for the conditions of Sweden. Under the conditions of northern regions and also those of dry years or summer drought, early varieties usually yield more on the average.

Practical experiments have shown the possibility of significantly increasing the productiveness of spring varieties by crossing them with winter varieties. For example, the best variety of spring wheat in Sweden, "Extrakolben" was obtained by crossing a spring variety with a typical winter variety "Queen Wilhelmina." This variety surpasses the better of the two parental varieties in yield by 10%.

Breeding for Drought Resistance:— Under the conditions of the continental dry climate of a great part of the agricultural area of SSSR, the development of varieties with drought resistance is exceptionally important. In breeding for drought resistance it is necessary to distinguish different kinds of drought and the time of their appearance, and to differentiate between soil and atmospheric dryness. For example, in Eastern Siberia the droughts affecting cereals are usually in the spring and fall; in regions where winter wheat predominates, as in the Ukraine and North Caucasus, drought usually occurs during the period when the crop is maturing. In regions where spring wheat predominates, in Trans-Volga and western Siberia, both spring and fall droughts are dangerous.

Most variable in the time of appearance of drought is the southeast European part of the Union.

Unfortunately, a characterization of the world assortment of wheats according to drought resistance can be made, thus far, only approximately, and principally on the basis of ecological-geographical data. Only recently has the construction of a physiological classification of wheat begun.

According to the usual accounts in the agronomic literature, drought-resistant forms of wheat are characterized by having few tillers and little leafiness. Awned forms appear to be more particularly drought-resistant. Investigations of physiologists in recent years have shown that drought resistance does not usually appear to be a specific character, constantly present in certain varieties. It is important to relate drought resistance to the phase of plant development, and to the previous conditions of culture. In relation to the length of developmental phase and to the time of occurrence of drought, this or that variety may appear to show different degrees of drought resistance. Breeding for drought resistance is necessarily associated with the conditions of development of the variety. The majority of the varieties which breeders consider to be drought-resistant do not appear so at all stages of development. For example, the 28-chromosome wheats of Arabia and Syria, which are exceptionally early, are usually planted in their native homes in the winter; they make use of the supply of soil moisture until it is exhausted at the beginning of summer and then they appear very resistant to drought. When sown in the late spring, they show little drought resistance if water is not ample. In the period of

heading, plants appear to be particularly vulnerable to drought; drought resistance in this case is very relative and is associated with rapid growth and planting at a time when moisture is favorable.

Another type is seen in the hard wheats of the Mediterranean region which pass through spring drought at an early stage, when they have a low level of vital activity which is the reason for their drought resistance. As a rule they are less resistant to later drought.

There is no one type of xerophily of wheat, but several types, characterized by a complex of specific characters and particular behavior.

To select and develop such physiologic types is one of the most important problems of variety physiology. Even at present, as a result of the work of I. V. Krasovskaya and N. L. Udolskaya (Omsk) we have a number of such types. For example, there are the early-ripening wheats of semi-arid regions (Syria, Arabia, Kazakstan) which are distinguished by their few tillers, little leafiness, and high degree of efficiency of the leaves. Here belong particularly the awned forms. The root systems of such wheats usually are rapid in development and deep; the grain is usually vitreous and characterized by compact structure of the tissues, thick veins, and sometimes small cells.

The second type of wheat described above, which is resistant to early drought, in all respects presents the opposite picture, with much leafiness, low assimilation, and leaves which, during the hot part of the day, when soil moisture is deficient, lose their turgor. This type is characterized by a well-developed root system which forms slowly (I. V. Krasovskaya).

The physiological investigations of I. V. Krasovskaya have disclosed extreme variation in drought resistance among the 28-chromosome wheats of Syria and Palestine (*T. durum horanicum* group) and also among the hard wheats of Asia Minor and other regions along the shores of the Mediterranean Sea; drought resistance also occurs in *T. timopheevi.*

The least drought resistance is found in the hard wheats of Abyssinia and the high mountainous regions of North Africa (Atlas region and Morocco). Low-growing forms of Morocco and Algeria are distinguished by a high degree of xerophily in comparison with varieties which are grown in the moist regions of the Atlas Mountains.

The most drought resistant soft wheats include the Siberian wheats and Volga varieties of the "Rusak" type (variety *erythrospermum*); also resistant are a number of varieties of spring wheats of Australia. Close to them in drought resistance is the Canadian "Marquis"; less resistant are the types "Poltavka," "Prelude," and "Novinka," and also early Indian spring varieties. The western European spring wheat varieties are not resistant.

The winter wheats that are particularly resistant to drought include "Cooperatorka," "Stepnyachka," and "Zemka." Less resistant to summer drought are "Ukrainka," "Kosobryukhovka," and "Durable." The majority of the western European forms, particularly the squareheads, are not resistant.

In the group of 42-chromosome wheats, there doubtless are forms surpassing our ordinary soft wheats in drought resistance. Particular attention should be given to the wheats of southwest Asia, Iran, Afghanistan, and Asia Minor. The most drought-resistant American forms of spring and winter wheats originally came from our region.

Breeding practice usually shows a low correlation between xerophily and productiveness in wheat. However, this correlation does not appear to be absolute and unchangeable; it is observed under normal moist conditions, yet its occurrence in the great world assortment still leaves much opportunity for breeding against drought.

In breeding for drought resistance it is essential to consider the ecotype of the plant in relation to the type of drought, and its distribution in the region, where breeding is being done.

Closely related to breeding for drought resistance is the selection of forms with *heat resistance.* Evidently the most interesting forms in this respect are those from hot regions, such as southwestern Asia, Iran, Afghanistan, and western China.

V. V. KOLKUNOV has found a correlation between anatomical-morphological characters, and the degree of drought resistance. He has directed particular attention to the size of cells and of stomata as important characters to aid in selection for drought resistance. In extreme variants in different groups and species of wheat, differences in the number and size of the stomata are actually very great. For example, in einkorns, which are distinguished by their high resistance to drought, the number of stomata in the field of vision of the microscope is twice as great as in ordinary wheats. SAX has noted an increase in the number of stomata with reduction of chromosome number in wheat species. The largest stomata and the fewest per unit area are found in soft wheats.

Differences in size and number of stomata are very striking when we compare extreme species and genera. For example, as shown by V. V. KOLKUNOV, in millet the stomata are very small in comparison with wheat. Within the narrower limits of species and varieties in which the breeder must constantly work, anatomical-morphological differences disappear and may not be used as criteria for discriminating between physiological types. Practical breeding experiments have not given any outstanding results in selection based on anatomical coefficients.

Varieties of wheat differ sharply in *root systems.* For example, according to the data of I. V. KRASOVSKAYA, the varieties "Milturum 0321" and "Caesium 0111" in the mature stage have roots weighing about 2.0 gm., while "Lutescens 062" and "Prelude" have root systems weighing 0.4 gm. We have no data on the inheritance of drought resistance in plants. There is no doubt that for obtaining highly resistant forms, the most promising procedure is to cross different ecological types, making use of species differences, particularly within the limits of species of the same chromosome numbers.

An important role in breeding for drought resistance must be played by direct testing of drought resistance under dry conditions, and also in irrigated culture in semi-arid regions by varying the amount and time of irrigation. In addition, the breeder must use the method of determining wilting coefficients and also study given varieties under different ecological-geographic conditions.

An important problem presented to the breeder by the irrigation of the Trans-Volga region is the new requirement in wheat type. Experiments to solve a comparable problem in Canada and the United States have not yet given definite results. This is associated with the short vegetative period in Canada. Many varieties such as "Marquis" and "Federation" are cultivated in both well-watered and dry areas. Under the conditions of Central Asia single varieties are sometimes cultivated both on dry land and on irrigated fields. On the other hand, as we have observed in Iran and Afghanistan in regions of old, settled culture, the highly productive forms of English wheat, *T. turgidum* are widely used on irrigated fields. In any case, irrigation opens up the possibility of selecting new and more productive forms.[90]

[90] VAVILOV, N. I. 1934. [Experiments in North America on wheat, and what we may learn from them. (On the problem of irrigation of the Trans-Volga).] Sotsial. Rast., VIR Leningrad. 15 pages.

Considering the possibility of lowered quality of varieties, from the standpoint of chemical composition and quantity of protein, in breeding for irrigated areas we must give attention to the selection of varieties with high quality. As shown by experiments in America and Russia on irrigated fields, irrigation is entirely compatible with high quality of grain and baking and milling properties.

Breeding for Winter Hardiness:— Under the conditions of the Soviet Union, breeding for winter resistance appears to be a basic condition for the cultivation of winter wheat. Our present assortment of wheats, including our best official standards, cannot be considered fully satisfactory although they are much more winterhardy than western European forms.

Winter injury to wheat has a number of causes: low temperature, the effect of soil crusting, freezing, standing water, and other factors. Although agrotechnical methods, such as cultivating in furrows, retaining the snow, good cultivation, and the use of fertilizer, are very essential in combatting winter injury to wheat, at the same time the variety plays a decisive role.

We can note certain geographic regularities in the causes of winter injury to winter wheat. In the Volga region the winter injury is due to low temperature and insufficient snow cover. In Ukraine and North Caucasus winter wheat is frozen by low temperatures, but also is killed out by somewhat less extreme temperatures, principally as a result of weakening of the plant from thawing and other causes. Not infrequently the damage to winter sowings is due to early spring droughts when the roots, in cold soil, are unable to furnish water to the leaves which are beginning to vegetate. In the northern, western, and central regions of the European part of the Union, winter wheat suffers from standing water under a deep snow cover. In the latter case, winter wheat is frequently damaged by the snow mold, *Fusarium nivale*.

For different regions the type of winter resistance must be different. For the Volga region it is necessary to produce the most freeze-resistant forms. For Ukraine and North Caucasus we must give attention to developing races of wheat with resistance to fluctuating winter and spring temperatures. For northern regions we must breed wheats that are resistant to standing water and fungi and to persistent snow cover.

Under the conditions of the United States the geographic differentiation of the causes of winter injury is very sharp, and this lies at the basis of practical breeding.

One of the most important findings of present-day plant physiology has to do with the relations between winter resistance of varieties and their preliminary hardening (N. A. Maximov, I. I. Tumanov). In an unhardened condition all wheat varieties, even the most resistant, are unable to withstand our rigorous winters. Even major differences in winter resistance of varieties may be demonstrated only when they are well hardened. I. I. Tumanov distinguishes phases of hardness: the first is with average daily temperatures from +6° to —1°; the second is the hardening in frozen plants at temperatures between —3° and —5°. For good hardening, as the experiments show, it is necessary to have a gradual transition from cold weather to light freezing. The rapidity and degree of hardening are not the same in different varieties. Varieties suffer at different temperatures in relation to the degree of hardness, in a range from —8° to —25°. The degree of hardening has no less significance than the intensity of freezing. From experience there are known cases of the killing of winter wheat at such temperatures as —14° and —17° C., which are entirely harmless to well-hardened plants.

Experiments with the great world assortment of wheats, carried out by the Institute of Plant Industry in Ukraine and North Caucasus, have shown that the most freeze-resistant forms are winter wheats of the Volga Region and Ukraine and, in part, wheats of the northern and central regions of the SSSR. Varieties of North Caucasus and Crimea are less cold-resistant. A low degree of freeze-resistance is characteristic of varieties of western Europe, Central Asia, and Iran, as well as the winter wheats of Trans-Caucasus, the Mediterranean region, and Argentina.

There is considerable freeze resistance in the wheats of the high mountains of southwestern Asia, particularly those growing at extreme altitudes (2600 m.).

Experiments have shown that, in general, our assortment of winter wheats, which mostly came from Hungary and the Carpathians, and the closely related types such as Banatka, are distinguished by the highest degree of freeze resistance. The United States wheats that were derived from ours have a high degree of winter resistance. The search among the present world assortment of soft and club wheats for the more winter-resistant forms is not an easy one. We have much opportunity for work in breeding for winter resistance.

Since winter damage often injures plantings only to a moderate degree, it is very essential, in breeding winter wheats for winter resistance, to give consideration to the possibility of regeneration in varieties. In this regard we observe marked varietal differences. For example, "Lutescens 0329" of the Saratov Station is very cold resistant but has weak regenerative powers.

To hasten breeding for winter resistance the present-day plant breeder calls the physiologist to his aid. In large breeding establishments, for testing varieties against low temperatures under artificial conditions, the workers with winter wheat use cold chambers. The indirect methods of determining resistance by osmotic pressure, dry weight, or sugar appear to have little promise for breeding practice.

With regard to breeding for resistance to thawing and other such causes, we have no data on varietal differences.

It is very essential to combine winter-hardiness and high yields in single varieties. In the great world assortment, in general these are negatively correlated. The varieties that are most resistant, such as 0329, unfortunately have low yields, but this correlation is not absolute and there is considerable promise for this type of breeding. In selecting for winter hardiness one must keep in mind the varied behavior of a given variety under different conditions. For example, the variety "Durable," developed at the Ukraine-Ivanovsk station, is comparatively resistant in Odessa where it is found in the first class for resistance; in western Siberia, and particularly in Leningrad, this variety drops to the second or even the third class. At present we do not have any fully-developed varieties which are entirely satisfactory for winter resistance and adapted to wide culture over large areas. Valuable varieties such as "Moskovskaya 2411" and "Durable" today are widely grown in the North, but these must be considered only relatively the most resistant.

The genetics of winter hardiness has been inadequately studied. Most significant is the work of NILSSON-EHLE, who first determined that the character of cold resistance genetically appears to be *polymeric,* based on a number of genes. This is shown by the complex picture of segregation in hybrids between cold-resistant and non-resistant winter wheats and the possibility of the appearance, as a result of crossing two non-resistant forms, of progeny which are more winter hardy; and the reverse, from two comparatively resisant forms not infrequently there are observed in the second or third genera-

tion progeny forms with less winter hardiness. For example, the winter-resistant variety "Minhardi" was developed by crossing two forms with less cold resistance (work of HAYES in the United States). Many crosses yield progenies with plants approaching the parental forms in degree of resistance. According to variety and combination of parents, winter-resistance appears at different times to be recessive, dominant, or intermediate. Dominance in this case depends on the combination of parental forms, the conditions of over-wintering, and, most of all, the conditions under which the display of winter resistance developed. Definitely recessive cold resistance in winter wheat was seen in the experiments of GAINES, SAULESCU (1931), and S. LEWICKI.

This may explain the occurrence of the most cold-resistant forms at the peripheries of the areas of winter wheat.

In the experiments of HAYES, in crossing the spring variety "Marquis" with the winter varieties "Minhardi" and "Minturki," susceptibility to winter injury was clearly dominant. The F_1 was totally destroyed when planted in the fall, differing little in this respect from the spring parent, while the winter parent under the same conditions survived entirely (Fargo, North Dakota).

Frequently the F_1 is intermediate in winter resistance. In different combinations of varieties of winter wheat behavior with respect to dominance is not uniform. This is particularly clear in the experiments of SAULESCU with 35 combinations. According to the experiments of HAYES, the spring form of life may be combined to some extent with high cold resistance.

ÅKERMAN (Svalöf) noted the appearance, in the progeny of hybrid winter wheats, of forms more resistant than the parents, with the most resistant lines characterized by a high content of sugar. The same thing was observed in the works of BROKERT in crosses of the winter wheat variety "Zemka" with "Cooperatorka" in Odessa and also at the Bezenchuksk Station (work of KOBALTOVA). Biochemical characters are usually associated with winter resistance (percent of dry weight and sugar); with respect to dominance and in segregation such characters behave in a similar fashion in winter resistance.

Mention of winter resistance in the foreign literature usually means freeze resistance. In the great majority of cases freeze resistance appears to be the basic factor, but considering the complicated nature of the resistance, as pointed out above, this involves much more than resistance to low temperatures.

The methods of studying the genetics of winter resistance have great significance in view of the complexity of such resistance and its relation to varied factors, such as hardening and the conditions of winter.

With winter hardiness, as with vegetative period or drought resistance, we must consider that this property, as many others, is associated with stage of development.

Resistance of varieties to freezing is determined by specific properties of the plasma-nuclear complex of the plant tissue cells. Fundamentally, resistance may be thought of as the ability of colloidal-chemical systems of the plasma-nuclear complex of plants to resist the destructive effect of freezing.

The concentration of sugars and salts, the quantity of water in the cells, the osmotic pressure, the acid activity, and other biochemical properties of the cell complex play a role in determining the degree of resistance in over wintering. In turn, these same factors also condition growth and development. In addition, morphological characters, such as the depth of coverage of the nodes and the quantity of reserve food substances in the plant, also have significance. There is particular importance in the ability of the plant to regenerate after injury. Winter resistance appears to be related to many other properties; it has been shown to be associated with drought resistance.

From this we can see the great difficulty in genetic evaluation of the factors; it is not easy to determine when we have pleotropic effects of different genes and when we are dealing with segregation of heritable factors. The ecological conditions of the experiments, as well as the ontogeny of the plant have much importance in changing the degree of freeze resistance.

As parents for crosses to increase cold resistance, we need to give particular attention to selection of ecotypes that differ in their behavior in different developmental stages, and of parental varieties that differ in their internal type of resistance while externally displaying resistance in the same fashion, and which have different reactions to the various overwintering complexes. In this respect wheats from different regions, with different winter conditions, are particularly interesting material. For example, the winter variety Polshi is comparatively resistant to freezing under conditions of the western and central European parts of SSSR. The Ukrainian and Crimean steppe varieties are also resistant to low temperatures.

Among the original varietal and species material, particular attention should be given to using as parents the most cold-resistant European forms of winter wheat, such as 02411, Durable, Lutescens 0329, Hostianum 0327, and others, the high-mountain Afghan club wheats which grow near the limits of possibility of winter wheat culture, and also the comparatively resistant forms of *T. spelta.*

There is particular interest in the winter varieties from western China (Kashgaria), where the winters are severe. The harsh open winter conditions occurring a little above sea level in Kashgaria and the use of winter varieties have evidently resulted in the development of particularly resistant types.

Cold resistance is also a property of some of the Siberian spring wheats, and high-mountain forms of Palmyra. These components may have a significant interest for transgressive combinations to obtain superior forms.

Among the group of 28-chromosome wheats we should pay particular attention to the winter-resistant forms of *T. dicoccum* (for example, var. *atratum*) and the cold-resistant spring Persian wheats (*T. persicum*).

Breeding for Response to Fertilization:— The ecological classification given above shows the marked differences in wheat varieties in their sensitivity to fertility and tillage of the soil. Experience long ago distinguished varieties of intensive and others of extensive culture. At the first Breeding Conference in Kharkov in 1911, P. P. KORKHOVA brought out the necessity of breeding varieties of cereals for intensive and extensive conditions.

Recent investigations in Sweden, Denmark, England, and Germany (LEMMERMANN, ÅKERMAN, GRANHALL, NILSSON-EHLE, HUDSON, and others) have brought out the marked varietal differences in wheat in sensitivity to mineral, and particularly to nitrogenous fertilizer.

Unfortunately the question of varietal differences in this respect has not yet been worked out for wheat as well as it has for barley. The outstanding success of Scandinavian, German, and English breeding of barley and, to some extent, of wheat during recent years is associated with selection of varieties which respond to mineral fertilization. In some cases there have been obtained striking results in increasing yields almost 20% as a result of selecting varieties which make particularly effective use of heavy fertilization. It is noteworthy that this work was done in regions where, without fertilization, the yields on the average have been 15 to 18 bushels per acre.

HUDSON (1934) in England experimentally showed the high sensitivity to fertilization of the improved variety Yeoman in comparison with the old variety

Squarehead Master. The Svalöf Station in Sweden has brought out marked differences in wheat varieties in their response to nitrogenous fertilization. Varieties with stiff straw were particularly reactive to such treatment.

P. ZAEV (1933) has determined a significant difference in the reaction of spring wheat varieties to different types of chernozem soil. In this work the natural soil differences were not obscured by fertilization. In his experiments the variety "Caesium 0111" was outstanding in its reaction to fertilization.

UDOLSKAYA (1932) in Omsk, under the conditions of a continental climate, found a particularly high response to fertilization in such varieties as "Milturum 0321," the hard "Gordenforme 010," and soft red wheat. KUDINOV (1926-1928), found that working with winter varieties of wheat, Cooperatorka made good use only of small quantities of phosphoric acid; "Stepnyachka," and to a somewhat less extent "Zemka," were more responsive to this fertilization.

Varietal differences in the use of fertilizer are determined by biological characteristics and differences in the root systems. The effects of fertilization vary in the different varieties. They include increase in tillering and production of heads, increase in weight per thousand grains, increase in size and weight of heads, increase in leafiness, changes in rhythm of development (SCHULTZE, 1928-1929), changes in the strength of the root system, etc.

The connection between response to fertilization and vegetative period is very complicated and is determined not only by varietal differences, but also to great extent by environmental conditions, quantity of precipitation, its distribution in time, and length of the vegetative period. The investigations of the Svalöf Station (NILSSON-EHLE) have shown that even in the conditions of a moist climate there is no definite simple relationship between the effectiveness of fertilization of different wheat varieties and their vegetative period. The comparatively early Australian variety "Aurora," under Swedish conditions, was most sensitive to nitrogen fertilization of all spring wheat varieties tested.

UDOLSKAYA (1934) has observed the great sensitivity to fertilization of the most drought-resistant varieties under Omsk conditions. It is interesting to note in the plot experiments of ZHEMCHUZHNIKOV, who was dealing with a large collection of ecological-geographical types, that the greatest sensitivity to fertilization also appeared in the drought-resistant hard wheats of Syria and Trans-Jordan.

It has been observed that there is a relationship, among varieties, between response to fertilization and overwintering (GREBENNIKOV, 1931).

The investigations of E. E. ZHEMCHUZHNIKOV (1934) in the Institute of Plant Industry, with different species and ecological-geographical types of wheat, have shown great differences in the varieties in their response on fertilized and unfertilized soils. Some varieties, for example the Argentina "Lin Calel" as well as the Canadian variety "Kitchener" and the hard wheat "Gordenforme 010," appear to be very productive without fertilization. Particularly responsive to fertilizer, as seen in yield increases, are the hard wheats of Asia Minor, Syria, and Trans-Jordan, as well as the soft Norwegian variety "Börsum" and the Russian "Novinka." Poor response is seen in the hard wheats, *T. durum hordeiforme* from Macedonia and *T. durum abyssinicum* var. *arraseita,* as well as in the Argentine "Lin Calel" and the Canadian "Kitchener," mentioned above.

The differential study of the reaction of varieties to environmental conditions, as reflected in quantity and quality of yields, which is particularly important in barley, has led to *the development of specific varietal agrotechniques and fertilization* adapted to individual varieties. Work along this line is going on at present in England, Germany, and Sweden in relation to brewing barley,

and it is very probable that in the near future this will also involve improved wheat varieties. It is entirely possible to develop varieties that are responsive to rather high amounts of fertilizer and which, when fertilized, increase their yields to profitably high levels, even when abundant nitrogen fertilizer is used (data from the Svalöf Station).

Despite the high productiveness of a number of old varieties under conditions of old-type agrotechnical methods and ordinary fertility levels, breeding practice in Sweden and Germany has shown that a number of newly-developed varieties significantly outyield the old ones when both are strongly fertilized with nitrogen. It has been proven that it is possible to create varieties with specific adaptation to high fertilizer norms.

The rapid increase in the manufacture of mineral fertilizers in Russia, the extension of agriculture to the north, the inevitable connection with the use of fertilizer, the extensive development of irrigated wheat culture in Trans-Volga which requires the use of fertilizers—all point to the rapid development in our region of wheat breeding for response to fertilization.

Breeding for Resistance to Lodging and Shattering:— In the past, when grain was harvested with the sickle, lodging in the field before harvest was comparatively harmless. The widespread change to the use of binders and combines presents a new varietal requirement that concerns both lodging and shattering. Resistance to lodging is based on different combinations of morphological and anatomical features of the straw and also relates to the conditions of culture, the density of sowing, moisture, quantity of precipitation, and nitrogenous fertilization. In the monograph by KRAUS, "Lodging of Cereals"[91] there is a detailed account of lodging in cereals, particularly wheat, and there is brought out clearly the relationship between lodging and light, fertilization, content of silicon in the plants, and other factors.

Of the varietal characters determining the degree of lodging there is much significance in the thickness of the stem walls, anatomical structure, brittleness of the straw walls, and solidity of the stem, which last is characteristic of hard and English wheats (*T. turgidum*). ZADE (1920) attached great importance to the height of the stems and area of the leaves.

KRAUS (1908) and WILLIS (1926) constructed instruments for measuring the thickness of straw. STUDTMANN developed field equipment for measuring lodging resistance of one or several plants. ALBERT and GABRIELLE HOWARD have related lodging resistance to development of the root system in wheat.

The varietal amplitude in wheat, in relation to lodging, is very wide, within both hard and soft wheats, and in this respect there are great possibilities. Such species as *T. compactum, T. sphaerococcum* and *T. spelta* have stiff, non-lodging straw and hence may be used for breeding purposes. A wide amplitude of varietal differences in lodging tendency is characteristic of *T. vulgare* and *T. durum*. Of the hard wheats, those of Palestine and Syria are most resistant against lodging.

For studying varietal differences in lodging, use can be made of strong fertilization with amendments of nitrogen and phosphoric acid (work of the West Siberian Breeding Station). Lodging is particularly frequent on highly fertilized fields and where a high seeding rate has been used.

As regards shattering, the amplitude of varietal differences in wheat is likewise very wide, within both soft and hard wheats and particularly in the first group.

In contrast to the southern Asiatic forms of soft wheat, having tightly-

[91] E. C. KRAUS, "Die Lagerung der Getreide." Stuttgart, 1908.

covered grain which can be threshed out only with difficulty, many of our ordinary European and Siberian varieties of soft wheat shatter easily, particularly under the conditions of a dry summer. Among these are observed extreme variants together with a whole series of intermediate forms.

Among the hard wheats we have a group of forms which easily shatter, in the mountainous regions of Atlas and Morocco. The hard wheats of Abyssinia, in contrast to the Mediterranean forms, thresh out quite easily.

In investigating the inheritance of shattering in some of the European wheats of the "Banatka" type which are widely grown in Poland, and the common western European awnless winter wheats, STEFAN LEWICKI came to the conclusion that the character of shattering in this group is dominant in crosses, and is conditioned by two or more genes.

The breeder is interested in developing non-shattering forms, but at the same time forms with grain which will not thresh with too great difficulty. Some wheat varieties have a tendency to breaking of the head at ripening, which also appears to be a serious defect.

Correlations in Wheat:— The study of correlations in breeding, the cause of which goes back to the principles of interrelationship between parts of organisms developed by CUVIER at the beginning of the 19th century, and the Law of Equilibrium of Organs of GEOFFREY ST. HILAIRE (1822), permeated all the breeding work of the second half of the 19th century and beginning of the 20th century. A great many investigations were dedicated to the question of correlations in wheat and a summary of these is given by CHERMAK in FRUWIRTH's "Handbook of Breeding" (4th ed., 1923).

Biometrics, giving very convenient formulas for expressing correlations by use of the correlation coefficient, stimulated work both from the standpoint of methods and from that of practical breeding.

In the chapter on wheat breeding by FRUWIRTH, RÖMER, and CHERMAK in the "Handbook of Breeding" mentioned above, a considerable section is devoted to an enumeration of correlations in wheat. Among the number of important correlations, CHERMAK notes: correlation of *tillering* with length of vegetative period, yield, and compactness of head; correlation of *number of stems* with *yield* of grain, length of head, and compactness of head; correlation of *stem length* with head length, weight of grain per head, and compactness of head; correlation of *stem thickness* with length of internodes; correlation of *grain yield* with head weight, grain weight, and grain size; correlation of *brittleness of head* with the tightness with which grains are enclosed by the glumes; correlation of *grain weight* with protein content and seed size; and finally, correlation of length of *vegetative period* with yield, grain size, and quantity of starch, protein, and gluten.

The enumeration includes both correlations within a single race and correlations involving differences between races of wheat. Some of the correlations have been subjected to particularly intensive investigations, *e.g.*, the correlation of length of vegetative period to yield and to protein content of the grain. Under the conditions of the favorable climate in western Europe and in England, usually a long vegetative period runs parallel with increased yields and, at the same time, with a lowered quantity of protein in the grain. Winter wheats usually yield more and have a lower percentage of proteins than spring forms.

Evidently there is frequently a connection, in moist temperature climates, between a long period from blossoming to ripening, and a low percent of protein. The factors which lengthen the period between blossoming and ripening,

as observations have shown, usually lower the percent of protein while increasing the yield. This may be the result of heritable differences in varieties in which the length of this period differs, but it may also be produced by conditions of weather, climate, and culture.

Many investigations have been conducted to determine such correlations in order to simplify breeding. In such work an attempt has been made to find one or a few characters to use as a basis for selecting desired strains.

The investigations of V. V. Kolkunov at the beginning of the 19th century brought out cell size and particularly the length of stomata, so-called "anatomical coefficients," as characters closely correlated with yield, drought resistance, winter resistance, and even quantity of nitrogen in the grain.

In recent times, the study of the free combination of heritable factors and the introduction of Mendelism has resulted in a basic revision of the concept of correlations in wheat. The great amount of new species and varietal materials in wheat discovered in the past decade in different regions, particularly in the areas of ancient culture and primary formation of races, has disclosed many exceptions to the former conception of correlations. Almost all of the correlations determined earlier have required a great limitation in the sense of narrowing the group of forms to which they apply, and in reduction of the correlation coefficients.

The crossing of forms, with investigation of the process of segregation, has wiped out many of the formerly accepted correlations. In the light of the great amount of new varietal materials and the data on hybridization, many of the correlations determined earlier have been found to have a multitude of exceptions.

At the same time, hybridological studies have revealed the presence of many genetic correlations due to the fact that a number of characters are determined by the effects of a single gene. In addition, many genes have pleotropic effects, as was brought out in the chapter on wheat genetics.

Investigations have shown that whole complexes, for example many characters of *T. spelta* and *T. compactum,* are due to individual genes. For example, there has been determined the linkage of genes for club head and awnedness in wheat.

Of the investigations in this field we may point out the work of A. A. Sapehin and his colleagues on the hybridological analysis of correlated characters in wheat (1916); in this work the genetic relationship between compactness of the head and other characters of the head was brought out very clearly.

Extensive investigations on correlated inheritance based on hybridological analysis have been carried out by Stewart in the United States (1927) and Boshnakian (1922). The investigations of Yu. A. Filipchenko have been particularly extensive and valuable from the standpoint of methods. He has worked out the index method for evaluating correlations, and has distinguished two types of correlations, *intrabiotypic* and *phenotypic* (within pure lines), which govern similar norms of reaction of two characters in response to the effects of the environment, and *intrapopulational* or *genotypic* correlations, in which the principal factor appears to be a relationship between biotypes forming part of the population. The first type of correlation is closely associated with individual variation. Populational correlations are associated with group changes.

In the work of Filipchenko we have a valuable contribution on the method of indexing which is often required in breeding work. This method has advantages over the use of absolute magnitudes only in those cases when the in-

dexes show regularities that are lacking in the absolute measurements or when the indexes are less variable than the absolute measurements. A lesser amount of variation in the indexes, in comparison with absolute magnitudes, occurs when the absolute values which are used in determining the indexes involve extensive correlations, and their variability under the effects of external conditions which are in a uniform fashion.

The method of correlation is gradually becoming used for interpreting the connection between quantitative equivalents of different plant characteristics. The biometric method is used to determine the degree of correlation in complicated inherited phenomena, but with heterozygous material, in the great majority of cases it may lead to errors. Practically—as we have seen from our survey of the basic directions of breeding for yield, drought resistance, winter-hardiness, and immunity—correlations have a comparatively limited significance, which requires us to depend basically on direct evaluation of plants. In particular, the studies of V. V. Kolkunov on the significance of anatomical coefficients, worked out with closely-related varieties, has shown that these coefficients do not apply in working with large assortments. At the same time, there is no doubt that the number of genetic correlations is bound to increase with increasing investigations in the field of wheat genetics.

Survey of the Present State of Wheat Breeding in Various Lands:— Extensive work in the breeding and genetics of wheat has unfolded during the past decades in a number of regions. This has been particularly noteworthy in Canada, United States, Argentina, Uruguay, Australia, Sweden, Germany, France, Italy, Poland, Finland, and Japan. In Africa there is particular interest in the work of breeders in Tunis, Morocco, Algeria, and South Africa. Breeding is also being done in other regions where wheat is cultivated, but still on a comparatively limited scale, principally by means of individual selection—for example in Hungary, Rumania, Bulgaria, Greece, and Portugal.

In previous sections of this paper we have outlined the results of breeding throughout the world, and here we will take up only the characteristics and objectives of work in the different regions and institutions.

Canada.— The great increase in wheat production in Canada, with the cultivated area increasing from 830,000 ha. in 1900 to 10,500,000 ha. in 1933, *i.e.*, more than tenfold, has been due in considerable part to the success of breeding. The scientific breeding of wheat has no doubt played a very essential role in the development of agriculture in Canada, bringing it, during the past decade, to first place in world wheat export. In Canada all breeding work on wheat has been centralized and carried out in the central experimental institute in Ottawa established in 1886. This experimental institution is well equipped and makes use of all present-day methods of investigation.[92] In addition we must note the recent (1932) opening of the Dominion experimental institute in Ottawa headed by the well-known scientist Robert Newton, who is recognized for his original work on the biochemistry and physiology of wheat varieties. This institute has interest because of its complex organization and inclusion of well-conducted sections of biology, chemistry, and physics. The Ottawa breeding institute, bearing the modest name of an "Experimental Farm," has produced some of the most noteworthy varieties of world wheat breeding. Wheat breeding here is associated with the names of the two Saunders, father and son (William and Charles), and today, with that of Newman. To

[92] The work of the Ottawa institute and other breeding institutions of Canada and also the organization of improved-seed production are described in detail in the book by V. V. Talanov, "Breeding, Seed Production, and Cereal Husbandry in the United States and Canada." Selkhozgiz, 1931.

characterize the Ottawa accomplishments, it is only necessary to mention such valuable spring wheat varieties as "Marquis," "Garnet," "Reward," "Prelude," and "Preston," which are world standards.

From the very beginning, the Ottawa institute has introduced a wide assortment of breeding materials, particularly from our regions, and from India and western Europe.

At the basis of Canadian breeding of spring wheat has been the Galician variety of soft wheat, "Red Fife," which was found in 1842 and is distinguished by its excellent grain under the conditions of the western prairies of Canada. Although it has valuable qualities, this variety did not have a sufficiently short vegetative period, and under the short summer conditions of Canada it frequently was injured by the early fall freezes which are common in western Canada.

This defect compelled William Saunders, beginning in 1886, to attempt to produce new varieties by hybridization of "Red Fife" with the Russian early-maturing varieties "Ladoga" and "Onega" and the Indian early varieties "White Delhi," "Hard Red Calcutta," "Gehun," and "Karachi." A particularly important role in shortening the vegetative period of "Red Fife," was played by the Russian "Ladoga," which was obtained from the region of Lake Ladoga near Leningrad. This early-maturing variety, like "Red Fife," was noteworthy for the high quality of its grain. Under Canadian conditions, it surpassed "Red Fife" in earliness by 10-15 days.

At the same time, "Ladoga" had low productivity which was not suitable for the Canadian requirements. and naturally hybridization was attempted, beginning in 1888. In this way there was obtained "Preston" which, on the average, matured six days earlier than "Red Fife." In later improvements the Himalayan variety "Gehun," which was collected at 11,000 ft. altitude, and the Russian "Onega" from the Archangel region, have played important roles. By crossing them there was developed the variety "Early Riga" which is 8-9 days earlier than "Red Fife." From "Early Riga" were selected "Riga M" and "Dawny Riga G," of which "Riga M" served as a parental form for one of the best of the present-day Canadian varieties, "Garnet"; "Dawny Riga G" was used for obtaining the variety "Ruby."

The greatest accomplishment of Canada, and we might say, of wheat breeding throughout the world, was the creation of the variety "Marquis." An epoch in the history of Canada is associated with the introduction of this variety into culture.

"Marquis" was obtained by crossing the early Indian variety "Hard Red Calcutta" with the Galician variety "Red Fife," which was done by William Saunders in 1892. The hybrids were planted from year to year, and in 1903 Charles Saunders began to give attention to one of the hybrid plants which he selected because of its good gluten (determining the quality of the gluten by a simple chewing of the grain). In 1907 "Marquis" was first increased on the experimental farm. In this cool year the wheat in Canada was particularly attacked by rust and "Marquis" was quite conspicuous for its resistance, stiff straw, excellent barrel-shaped grain, high flour yield, and fine bread-baking quality. In 1915 "Marquis" occupied 90% of all of the area in spring wheat in Canada and was widely distributed in the northern United States.

"Marquis" ripens from 3-10 days earlier than "Red Fife," depending on region and season, and is distinguished by non-shattering, high yield, and resistance to loose smut. The high quality of grain and flour from "Marquis" at once raised the standard of wheat required for the world market (see Fig. 33, p. 347).

Of the other interesting Canadian varieties we must note "Prelude," a complex hybrid of Galician, Indian, and Russian northern wheats (see its pedigree in the chapter on selection of parental pairs). "Prelude" ripens 1-2 weeks earlier than "Marquis." The variety "Garnet" is interesting for the fact that while surpassing the parents in earliness, it equals or even exceeds the yields of the parents. Its genealogy is also very complicated, as may be seen from the table given in the section on parental pairs. The original cross was made in 1888.

"Garnet" ripens 6-12 days earlier than "Marquis." Introduced into culture in 1926 it became rapidly distributed and occupied a region to the north of "Marquis." Although it does not equal "Marquis" in grain and flour, nevertheless it belongs in the group of wheats considered to have grain of high quality.

By crossing "Prelude" with "Marquis" in 1912 there was obtained the new variety "Reward" which ripens a week earlier than "Marquis." In vegetative period it occupies an intermediate position between "Marquis" and "Prelude." This variety is distinguished by its milling and baking qualities. It even surpasses "Marquis" in quality of the protein. Its basic defect is a comparatively low productivity in a number of regions.

At the present time in Canada "Marquis" occupies about 70% of the spring wheat acreage, "Garnet" 20%, and "Reward" and other varieties 10%.

Very interesting cytogenetic work on interspecific hybrids of wheat in Canada has been done by THOMPSON in Saskatoon, as we have discussed in the chapter on interspecific hybridization.

Extensive work on the immunity of wheat from diseases is concentrated in the Dominion Rust Research Laboratory in Winnipeg where at the present time there are working a large number of phytopathologists and breeders (CRAIGIE, MARGARET NEWTON, GOULDEN, and others).

Until recently all of the Canadian breeding work was centralized in Ottawa, with hybrid materials planted in various regions in a network of experimental stations; only in recent years has there been a partial decentralization, with autonomy in the special work at Winnipeg.

The greater part of the work in Ottawa has been concentrated on spring wheat, which occupies in Canada an acreage of 10,000,000 hectares. Winter wheat does not succeed in Canada despite extensive work and a great interest in introducing it into culture. The area planted with winter wheat is only about 350,000 hectares.

The principal objectives of Canadian spring wheat breeding at present are to develop resistance to fungus diseases, early maturity, and grain quality.

Even "Marquis," which approaches the ideal from the standpoint of productivity, resistance to a number of diseases, excellent grain quality, non-lodging, and non-shattering, is not satisfactory in Canada because of its susceptibility to stem rust.

Exporting a large part of its wheat crop, Canada is very well organized to standardize its wheats according to the rising requirements of grain quality on the world market. Every year tens of thousands of analyses for protein are made, and valuable maps of protein production have been published. (Winnipeg Laboratory).

Canada is characterized by the small number of varieties and the governmental organization of breeding and seed production.

Because of its originality and fundamental character, attention should be given to the work of the Winnipeg Station on resistance to rusts and smuts. We should mention the investigations of CRAIGIE who first discovered the role of hybridization in the production of physiologic races of rusts and smuts.

Extensive work has been done on physiologic races. Here we also find original investigations on the genetics of immunity from rusts and smuts.

United States of America.— While in Canada all the breeding work is concentrated in governmental experiment stations, in the United States, along with experimental institutes concerned particularly with methodological work, practical breeding has also been done by private firms. To be sure, in the case of wheat the role of private firms in America is considerably less than with other crops.

Nevertheless such work has been widespread, and this is associated with the great diversity of varieties cultivated in the United States. The lists published by the Department of Agriculture include more than 100 varieties of commercial significance. Actually, as indicated in the "Yearbook of the Department of Agriculture," in 1933 the number of wheat varieties in agricultural production reached 300.

Experimental work as well as breeding has reached a high stage of development in the United States. There are breeding stations in nearly all of the experiment stations in the various states, which are well-organized and can make use of present-day methods of physiology and phytopathology. Each station publishes regular reports in which are described the valuable materials for wheat breeding. A number of the stations have additional experimental fields in different regions. Phytopathology in particular has been developed to a high level in the breeding stations; in this respect, until recently, the United States was the leader in world breeding. STAKMAN in the University of Minnesota (St. Paul) first began investigations on physiologic forms of rust. The cooperative work of breeders and phytopathologists and recently, physiologists, is characteristic of American breeding.

The greater part of the wheat in the United States consists of soft winter and spring wheats which are grown on about 22,000,000 hectares, with 1,500,000 hectares devoted to durum wheat (principally in the Dakotas, Montana, and Wyoming). An area of about 500,000 hectares is occupied by club wheat in Arizona, Utah, Nevada, and California. In contrast to Canada, the greater part of the acreage of U.S.A. is in winter wheat.

Wheat breeding work is concentrated principally in the States of Minnesota, North and South Dakota, Washington State (Pullman), Nebraska, Kansas, and California. In Minnesota (St. Paul) the leader is Dr. HAYES, author of the well-known handbook on breeding agricultural plants, who has produced a number of winter-hardy forms of winter wheat, and has made extensive use of interspecific hybridization. He has developed the most winter-hardy varieties for the conditions of the U.S.A. such as "Minturki" and "Minhardi," and this has made possible the extension of the cultivation of winter wheat 150 kilometers farther north in regions where only spring wheats were previously grown. In South Dakota MCFADDEN's pioneering work was done on crossing species of wheat to obtain immunity from rust and smuts. By crossing soft wheat with emmer, he developed varieties which are resistant at once to stem and leaf rust and to loose and covered smut. One of these varieties he named "Hope." There is no doubt that this variety has great interest for breeding in other regions, for making use of its complex of immunity. Recently this variety has been used in SSSR for producing immune varieties of soft wheat.

In North Dakota and in Montana particularly valuable work on spring wheat has been done by Dr. WALDRON who produced, by crossing the varieties "Marquis" and "Kota," the new, outstanding variety of spring wheat "Ceres" which is resistant to stem rust.

In the State of Washington investigations have been carried out under the leadership of Dr. GAINES, particularly in the development of varieties that are immune from smut.

In Kansas much work has been done under the direction of Dr. PARKER. Here is principally concentrated the work on winter wheat. The work is particularly directed at drought resistance and resistance to fungus diseases, as well as to Swedish and Hessian flies. Likewise there have been extensive investigations in breeding winter wheat in Nebraska under the direction of Dr. KIESSELBACH.[93]

We must note the interesting work on resistance to *Fusarium* diseases done in the University of Wisconsin at Madison in charge of Dr. DICKSON. In the Cornell University Institute of Breeding there has been activity in studying the methods in wheat breeding directed by Dr. LOVE.

Almost all the stations have worked extensively from a methodological standpoint in studying milling and baking quality of varieties. Particularly original work of this sort has been conducted by the Department of Agriculture in Washington, and also in Minnesota and Kansas. In Minneapolis this work has been led by BAILEY, the author of the outstanding book "Chemistry of Wheat Flour." We must mention the work on breeding under irrigated conditions conducted in the states of Colorado, Montana, and California.

A synthesis of all of the investigations in the United States, with a systematic study of varietal diversity, and also methodological work on hybridization between distantly related parents, as well as all the work on governmental variety testing, is accomplished by a small group of investigators in the Bureau of Plant Industry with headquarters in Washington, led at present by Dr. CLARK (up to 1931 this was in charge of Dr. LEIGHTY). This is the principal source of information from which one may quickly learn what is being done with wheat in U.S.A.

Argentina.—The development of railroads deep into the Pampas has stimulated an extension in wheat planting from 3,250,000 ha. in 1900 to 8,600,000 ha. in 1931. Along with this, in the past decade there has been a significant increase in yields which is principally due to the accomplishments of breeding; this has involved not only breeders, but also economists (T. H. BRINKMANN). Basically this is a region of soft wheat cultivation; very rarely hard wheats, principally of the variety "Candeal," are grown.

The breeding work in Argentina at present is largely being done in the following institutions: the private firm of Dr. E. KLEIN in the province of Buenos Aires; the experiment station in the South Pampas in Tres Arroyos under the direction of BRUNINI; the experiment station in Pergamino; and the experiment station in Guatrache (Central Pampas) under Dr. WILLIAMSON who has worked with the hybridization of wheat and rye in the Central Pampas. Until recently breeding was also being done under the direction of Dr. RUDORF near Buenos Aires.

The greatest accomplishments in wheat breeding are associated with the names of two Englishmen, BATESON's student, W. O. BACKHOUSE, who developed the variety "38 MA," and Dr. FISCHER, who is now working in Uruguay.

Until recently wheat breeding in Argentina has been conducted principally by German, Italian, and English scientists.

Beginning in 1912, the Ministry of Agriculture organized the section of Breeding and Genetics for improving Argentine wheat. At first the work was

[93] V. V. TALANOV, "Breeding, Seed Production, and Cereal Husbandry in U. S. A. and Canada," Selkhozgiz, 1931.

by means of individual selection. As a result we have the varieties "Lin Calel" and "Barleta 23." Of the introduced foreign wheats, the Kansas variety of winter wheat "Kanred" is particularly well adapted to the conditions of Argentina. BACKHOUSE began systematic work on hybridization in 1931, principally using for parents in his crosses Barleta and a Chinese variety which was resistant to shattering and to stripe rust. As a result he developed the outstanding variety "38 MA" which is now widely grown in Argentina.

E. KLEIN has made extensive use of hybridization in recent years, producing the varieties "Record," "San Martin," "Triunfo," "Klein 32," and "Klein 33."

A majority of the new varieties cultivated in Argentina have been created by crossing. In addition to the varieties mentioned above, the early-maturing Italian variety "Ardito" with short straw has been used in hybridization. Particularly valuable characters of new Argentine varieties are their non-shattering and adaptation to combine harvesting, which is very extensively practiced in all Argentina. In recent times the new varieties Klein 32 and Klein 33 have become widely cultivated.

Ecologically the wheats of Argentina are comparatively uniform and RUDORF has divided them into three groups, based mainly on earliness of maturity. In 1935 the Ministry of Agriculture in Argentina published detailed maps of the regional distribution of wheat varieties.

In recent years breeding has aimed particularly at productiveness, resistance to stripe rust, and high quality grain. Evaluation of wheat for milling and baking quality in Argentina has reached a very high level; it is led by the French investigator ANDRÉ, who is in charge of the well equipped laboratory of the Ministry of Agriculture in Buenos Aires. With respect to immunity from rust, extensive work has been done prior to 1934 by Dr. RUDORF; immunity from smut and physiologic races have been studied by NIEVES in the Central Pampas.

Uruguay.— Little Uruguay has a first class experimental institution conducting intensive work on wheat breeding under the directorship of Drs. BOERGER and FISCHER. The breeding station La Estanzuela Agricola located in southern Uruguay, 25 kilometers from the city of Colonia, has been appropriately called the South American Svalöf. The significance of the work of this station extends far beyond the limits of Uruguay, and is particularly important for understanding the conditions of breeding in Argentina. We might say that the wheat region of Argentina extends into southern Uruguay. The Uruguay station has done extensive work on hybridizing wheats to develop quality and for immunity. Work on wheat hybridization here was begun by Dr. KLEIN who at present is working in Argentina.

The published report of BOERGER, "Sieben La Plata Jahre" (1921) and particularly the report of his 15 years of work, "Observaciones sobre agricultura. Quince años de trabajos fitotecnicos en el Uruguay," is a classic on breeding and has significance not only for Uruguay, but also for Argentina.

Chile.—Wheat breeding in Chile is conducted in three institutions, the experiment station near Santiago in Llano Subercaseaux, the agricultural section of the Ministry of Agriculture in Santiago (directed by Dr. KALT), and the experimental field in Temuco (in southern Chile). The experiment stations belong to the National Agricultural Association, and were founded in 1924. The culture of wheat in Chile is of comparatively recent origin, and there are no old local varieties. All of the wheat culture is based on the introduced Argentine, Uruguayan, Australian, and Italian varieties. Experiments have shown that certain Australian varieties (*e.g.*, "Yandilla King") are par-

ticularly suitable here; of the varieties from Uruguay an outstanding one is "Artigos" which was developed by Boerger and is distinguished by its non-shattering and rust resistance. The principal breeding work in Chile consists of a study of the world assortment under the conditions of this region, and a selection of the most valuable and suitable varieties, their increase, development of pure lines, and organized variety tests. The conditions of central and southern Chile are particularly favorable for wheat culture. Recently the Experiment Station in Santiago has begun hybridization.

Australia.— In recent years the area of wheat cultivation in Australia has reached 5,870,000 hectares (1933). Breeding work with wheat in this region had reached a high level long ago. There is probably no region where intra-specific and interspecific hybridization of wheat has been so extensive as in Australia. The work of Farrer on hybridization goes back to the end of the 19th century, when he began to cross distinct geographic races and species on a broad scale. His work, "Making and Improvement of Wheats for Australian Conditions," published in 1898, still has interest. An outstanding feature of the Australian breeding work is its good documentation.

The unfavorable climate of Australia, with frequent droughts, fungus diseases, and low yields, has required breeders to make extensive use of hybridization. There have been made literally thousands of different combinations, with wide use of the great world assortment of wheats.

In the official list of Australian varieties published in 1933, the extent of hybridization of wheat in Australia may be seen clearly. For this reason wheat breeding in Australia deserves special critical study. As a result of hybridization there have been created a great number of valuable varieties distinguished by their stiff straw, productive heads, and comparative earliness. All varieties of Australia are of spring type. Among them the most widely grown in recent years has been "Hard Federation" which was derived by individual selection from the noteworthy variety "Federation." This last variety, in turn, was developed by Farrer in 1901 by crossing Indian, Galician, and American varieties, and up to this time it is still widely grown, particularly in Victoria and New South Wales. Also widely distributed are the varieties "Bunyip," "Nabawa," and "Gluyas Early."

The number of improved varieties listed in the official catalog reaches 200, which includes, along with those developed by the experiment stations, some produced by private seed firms concerned with wheat breeding.

In recent times the Australian breeders have made common use of the latest methods of physiology, including the regular electric lighting in the field for hastening the vegetation of northern varieties, constructing for this purpose special electric installations in the breeding fields. Cooperative work with phytopathologists has led to extensive breeding for resistance to rusts and smuts. Along with the ordinary species of smuts there is also found here the leaf smut, "flag smut," against which a number of resistant varieties have been developed ("Bunyip," "Florence," and others).

It is interesting to note in the Australian breeding work the extensive use of anatomical methods in evaluating grain and straw in connection with selection for non-lodging. Anatomical investigations of wheat varieties made in Australia by Cobb and others represent a great contribution to the knowledge of wheat anatomy.

South Africa.— South Africa resembles Australia in its climate in the regions where wheat is cultivated, and, accordingly, much use is made of the results of Australian breeding. In recent times this has been supplemented by hybridization work to improve the Australian varieties.

India.—During the last 20 years much has been done here by ALBERT HOWARD and his wife, GABRIELLE HOWARD. In 1909 A. HOWARD published the excellent monograph, "Wheat in India," in which there were first described the diverse Indian wheats. The region of wheat cultivation in India is concentrated in the northwest, principally in the United Provinces and in Punjab, Sind, and Bihara. The wheats of India are principally subspecies of *T. vulgare;* rarely hard wheats and club wheats are grown, and *T. dicoccum* is infrequently found in cultivation.

At the present time, approximately 10% of all of the area occupied by wheat in India is planted with improved varieties developed by the Agricultural Experimental Institute in Pusa directed by A. HOWARD. The improvement of wheat has involved both the selection of forms from local Indian varieties and the use of hybridization, with particular attention to grain quality and to the root system.

The Indian varieties are distinguished by their early maturity, good grain, low growth, and non-shattering. The drought-resistant forms "Pusa 4" and "Pusa 12," are quite widely distributed; the latter is unusual in having bright red grain which permits it to be easily distinguished from other varieties. "Pusa 12" also is grown in Argentina; "Pusa 4" is cultivated at present in Australia. "Pusa 12" and "Pusa 4" were developed by individual selection. Of the new hybrid forms, Pusa 52, 54 and 100 are becoming widely distributed.

In India breeding work is also being done in Punjab as well as in Pusa.

In 1933 the wheat area in India amounted to 19,350,000 ha.; about half of this was under irrigation.

China and Manchuria.— The area in cultivated wheat in China, together with Manchuria, exceeds 20,000,000 ha.

Despite the great significance of this crop for China, which is exceeded only by rice, the great mass of the wheat consists of populations of old local varieties, primarily of soft wheats. In some parts of China, farmers deliberately sow mixtures of varieties, considering that some varieties are more suited to wet years and others to dry ones. The subspecies of Chinese soft wheats, as shown by studies of several hundred samples carried out by Dr. LOVE in China, present a great diversity, including, along with ordinary awned and awnless forms, rare inflated and short-awned forms and also subspecies with black glume edges. This is evidently associated with the antiquity of wheat culture in China, although originally the crop was introduced from southwestern Asia.

HOSONO (1935) studied 426 specimens of Chinese wheat obtained from a majority of the provinces where wheat is cultivated, and found 26 botanical subspecies of soft wheats, 9 subspecies of club wheats, and, as rare mixtures, *T. durum hordeiforme* Host. and *T. turgidum lusitanicum* Kön. Among these there is particular interest in the new, entirely awnless subspecies of inflated soft wheat, the variety *huangyangense* Hosono.

The ecological picture of the wheats of China is very complex, corresponding to the diversity of cultural conditions. Among these wheats we find forms with high resistance to stripe rust, together with a number of forms that are very severely attacked by this fungus. Many of the varieties of soft wheat are distinguished by their early maturity, short straw, and non-shattering.

A number of Chinese varieties have been used by the breeder BACKHOUSE in improving Argentine wheats. The squarehead forms of wheat with stiff, low straw have particular interest.

In recent years, near Nanking in the agricultural college there has arisen a breeding station in the organization of which the well-known American breeder Dr. LOVE participated. The workers in this institute, CHEN and SHEN,

have published on the inheritance of quantitative characters in wheat, on immunity from specific Chinese diseases, and comparing 537 foreign varieties with Chinese local forms.

Notwithstanding the probability that the ancient Chinese culture has resulted in the development of more valuable forms of wheat, the recent breeding work has produced varieties surpassing local forms in yield by 30%.

The breeders have used both the method of individual selection and that of hybridization. Out of local samples there were isolated 15,000 pure lines. From these were developed a number of valuable varieties, such as 2905. Varieties obtained by crossing are already being increased (1691 and 2634). Great attention has been given to breeding for resistance to leaf smut and nematodes.

The wheats of Manchuria have been described in detail by B. V. Skvortsov (1927). To a considerable extent they are varieties introduced in the past from Russia. These are principally forms of soft wheats (*albidum, lutescens, milturum, erythrospermum*) and rarely club wheats (*T. compactum* var. *icterinum* and other subspecies); very rarely hard wheats are cultivated here.

The Manchurian Experiment Station has developed a number of varieties by individual selection ("Telin," "Sansin," "Livingston," "Anda," and others).

The area occupied by wheat in Manchuria was 1,380,000 ha. in 1931.

Japan.— As in China, the Japanese wheat acreage is exceeded considerably by the cultivation of rice and barley, nevertheless 500,000 ha. are occupied by wheat, and this area tends to increase. The Japanese wheat varieties, like the Chinese, have specific peculiarities: low growth, stiff straw, and marked earliness. Ordinarily they are sown here in the fall. At this time old local varieties are cultivated principally and these are in the form of rather uniform populations.

The center of research is the University of Kioto, where, under the leadership of Professor Kihara, valuable studies on the cytology and genetics of wheat have been conducted. The very interesting cytological work of Sakamura was done in the University of Sapporo on Hokkaido Island. In the field of cytology and cytogenetics the work of the Japanese investigators has exceptional interest. They were the first to distinguish the three groups of wheat according to chromosome number, in the school of Kihara, and the particularly detailed cytological analyses of interspecific and intergeneric hybrids by Kihara and Lilienfeld revealed the specific genome of *T. timopheevi*. We must take note also of the valuable review of Matsuura on wheat genetics. Although Japan has not done much original work in wheat breeding, in the field of cytogenetics it occupies an outstanding position. In recent years a large part of the investigations have been reported in the journal "Cytologia" published in Tokyo in English and German.

North French Africa.— In North French Africa extensive breeding work with wheat has developed only in recent years, principally in Tunis under the leadership of Boeuf and in Rabat in Morocco under the direction of Miège. Boeuf's recent monograph on wheat breeding has exceptional interest because of its broad scope. It covers not only breeding, but also botanical investigations of wheat with the use of all present-day methods. The leading objective of the work in Tunis is to create non-lodging forms that are resistant to summer drought and also to rust. The work involves soft and hard wheats. In Algeria the activity is principally limited to a study of varieties. Breeding is done on a small scale in the agricultural college under the directorship of Professor Ducellier. There is particular interest to us in the numerous varieties

of North African hard wheats. Up to this time they have occupied a dominant position here (in Algeria three-fourths of all the wheat acreage).

England.— England is a region of long-established wheat breeding work. Its beginning goes back to the first half of the 19th Century when, in some unknown manner, there appeared the first squareheads in England, having high productivity and stiff straw, but at the same time producing grain of low quality. In the second half of the 19th Century there began extensive breeding work with squareheads.

The history of English wheat breeding is associated at the beginning with the names of Colonel LE COUTEUR, Major HALLETT, and PATRICK SHIREFF. All three documented their works with detailed tracts which, even to the present, have historical interest in world breeding.

LE COUTEUR, under the influence of the Spanish botanist LA GASCA, who had emigrated to England, began wheat breeding by individual selection.[94]

HALLETT, in the middle of the 19th century, introduced the classic pedigree method of repeated selection, choosing heads from the best plants, and among the heads, those with the best grain, conducting his work on fields of the most uniform fertility possible. We should note that some of HALLETT's varieties have survived in England up to the present time.

Persistent breeding work in the middle 1800's was begun by PATRICK SHIREFF and continued for many years, his selections resulting in a number of valuable wheat varieties; his hybridization work did not have great success. In his book, "Improvement of the Cereals and an Essay on the Wheat-Fly" (1873), he relates in detail the methods of his breeding. In the chapter on hybridization is outlined the history of the first wheat crosses made in England.

Extensive work on wheat hybridization began in England with BIFFEN, in Cambridge, toward the beginning of the 20th Century. He studied the problems of wheat genetics and analyzed the inheritance of wheat characters according to MENDEL's law. He was the first to determine the Mendelian behavior of resistance to fungus diseases, grain quality, and also other physiological characters. Many of his findings were later subjected to important modifications. The process of segregation of physiological characters is much more complicated than BIFFEN supposed, but in any case, to him belongs the priority for having determined the Mendelian behavior of a majority of wheat characters, both morphological and physiological.

The varieties developed by BIFFEN became widely distributed, and his work, as well as that of his assistant ENGLEDOW, on the theory of breeding wheat, has significant interest in the world breeding literature. In a small book, BIFFEN summarized the results of his twenty years of breeding work and this has valuable original data, of particularly practical character. A short summary of wheat varieties in England and also of the history of breeding was published in 1934 by PERCIVAL. Variety testing work has been done at the Institute of Agricultural Botany in Cambridge.

Germany.— A detailed review of the history of breeding field crops in Germany was published by Dr. HILLMANN in 1910,[95] in which is given a résumé, not only of the work of the experiment stations, but also of all of the principal private seed firms; the book contains valuable data on wheat breeding. Supplementing this work, in the study of the history of German breeding, is the RÖMER Festschrift of the Gesellschaft zur Förderung deutscher Pflanzenzucht, published in 1933.

We can agree with Dr. HILLMANN that at the beginning of the 20th Cen-

[94] LE COUTEUR, J. "Varieties, properties, and classification of wheat." Jersey, 1836.
[95] "Die deutsche landwirtschaftliche Pflanzenzucht," Berlin, 1910.

tury German scientific breeding occupied first place, both as to the number of well-organized governmental breeding institutes, and to the great amount of practical work done by seed firms, creating a world reputation for German breeding.

WILHELM RIMPAU in Schlanstedt, proprietor of a small seed firm, is considered the father of scientific breeding in Germany, as is the seed firm VILMORIN in France. His work in breeding goes back to the third quarter of the 19th Century. His classic studies on hybridization of cereals, particularly wheat and barley, have not lost significance to the present time ("Kreuzungsproducte landwirtschaftlicher Kulturpflanzen," Landwirtsch. Jahrb., 1891, and "Die Züchtung neuer Getreidevarietäten," *ibid.*, 1897).

The original good handbooks on wheat breeding were published in Germany. First we must note the important book by FRIEDRICH KÖRNICKE, "Handbook of Cereals" (1885) in which, in two volumes, is concentrated the knowledge of the wheat varieties of the world so far as known at that time. This work still has significance and is a classic in the world literature on wheat. We must also mention the book of RÜMKER on the methods of breeding cereals. Until recently the basic handbook for studying wheat breeding was the 4th volume of the capital collection of works, "Handbuch für Pflanzenzüchtung," published under the editorship of the Austrian breeder FRUWIRTH, which appeared in Germany in a series of editions, beginning in 1900.

We cannot fail to mention a number of German scientific journals, for example, Kühn Archiv, Zeitschrift für Pflanzenzüchtung, Beiträge zur Pflanzenzucht, and Der Züchter, in which are accumulated a large number of valuable papers on wheat breeding.

German breeding until recently was primarily in private hands, however long ago the foremost commercial firms of Germany began to apply science to their work, and the breeding of a number of the larger seed firms was carried out on the level of contemporary science. It is characteristic for all Germany and up to this day, for there to be a large number of seed firms engaged in practical breeding and competing with one another.

Of the largest of these firms, we should mention the following:

GUSTAV BESTEHERN (Belitz bei Cönnern a. Saale, Prov. Sachsen).
RUDOLF BETHGE (Schackensleben, Prov. Sachsen).
FERDINAND HEINE (Kloster Hadmersleben, Bez. Magdeburg. Prov. Sachsen).
GUSTAV JAENSCH & Co. (Aschersleben).
W. RIMPAU (Schlanstedt, Bez. Magdeburg).
C. BEHRENS & Co. (Schlanstedt).
FR. STRUBE (Schlanstedt).
BESELER (Anderbech, Prov. Hannover).
A. KIRSCHE (Domäne Sundhansen, Herzogtum Gotha. Thüringen).
PH. HEINRICH STOLL (Meckerheim, Baden). (Of particular interest here is the breeding with *T. spelta*).
ARNIM CRIEWEN (Criewen b. Schwedt, Brandenburg).
OTTO CIMBAL (Frömsdorf, Schlesien).

The list of cultivated wheat varieties in Germany is very long, no less than 200 varieties for this comparatively small region where about 2,300,000 ha. (1933) are devoted to wheat. Voss in his "Varieties" lists 155 varieties of soft wheat having practical significance in Germany. HILLMANN's review mentions 61 private firms working with winter wheat and 28 firms working with spring wheat.

The work of the German firms, in the past and present, has involved both individual selections from local and foreign varieties and extensive use of hybridization.

A particularly important role in improvement of the German varieties has been played by the English squareheads, and to some extent the improved varieties developed at the Swedish Svalöf Station.

In addition to work of the private firms, important breeding in Germany has been done in governmental breeding stations which were either independent or, more frequently, experiment stations attached to agricultural institutes and universities.

Of the governmental institutions working with wheat breeding we should first mention the agricultural institute in Halle, at the University, which in the past has been directed by WOLTMANN and HOLDEFLEISS and at present by RÖMER. In the past, and particularly in the present, the work of this institute on breeding methods has exceptional interest because of its fundamental analytic nature and the fact that it combines the work of physiologists, breeders, phytopathologists, and technologists.

An excellent summary of the accomplishments of the Institute of Breeding in Halle is given in a special volume, the 50-year Festschrift for RÖMER in the journal, "Kühn Archiv" (1933).

Imitating the basic methods of breeding for immunity in the United States by inviting Dr. STAKMAN of Minnesota to assist in doing this, the Institute in Halle has conducted extensive studies of physiologic races of rusts and smuts and has begun a systematic hybridization of wheat for the purpose of developing immune varieties. This work is directed by RÖMER and is prominent in present-day breeding literature.

Here we must emphasize the work at Halle in studying grain quality by using small probes with a special method worked out for this (PELSCHENKE method). Recently there has been work here on varietal physiology, under the direction of Dr. FUCHS.

Of the other large breeding institutions we must note the work of the Bavarian station in Weihenstephan near München, formerly directed by Professor KRAUS, the author of the book on cereal lodging, and later by Professor KIESSLING and Dr. RAUM.

The Institut für landwirtschaftliche Pflanzenproduktionslehre in the University of Breslau has pioneered in European scientific wheat breeding. Here began the work of RÜMKER, author of one of the best books on the methods of breeding cereals, and originator of a number of wheat varieties. At present Dr. BERKNER, who has worked on the ecological classification of wheats, is located here.

The breeding station in the Agronomic Institute of the University of Jena has been working on wheat breeding for a number of years. Until lately this work was directed by Professor EDLER.

Important work on wheat breeding in the recent past has also been done at the Agronomic Institute of Leipzig University under the direction of Dr. ZADE, who first used the method of sero-diagnosis for distinguishing wheat groups.

We must also note the limited, but original work on wheat of one of the most interesting breeding establishments in Europe, created by Dr. ERWIN BAUR in Müncheberg near Berlin. At this institute many interspecific and intergeneric hybridizations have been made, and wheat varieties suitable for sandy and light soils have been developed.

In Tyrol, in the region of Württemberg in Bavaria, where up to this time a considerable acreage has been used for the cultivation of spelt, many private firms have conducted hybridization work, crossing spelt with soft wheat principally for the purpose of increasing the productivity of spelt and reducing its brittleness.

The work of Dr. WACKER in Hohenheim has been of a similar nature.

Finally we must mention the institute in Bonn-Poppelsdorf where F. KÖRNICKE and WERNER have carried on their studies of wheat systematics.

Of the recent work in Germany there is particular interest in breeding wheats for response to mineral fertilization, immunity from rusts and smuts, and also quite recently, for milling and baking quality. The German institute for studying milling and baking quality of cereals (Reichsanstalt für Getreideverarbeitung) in Berlin is one of the first in origin and in facilities. The results of investigations at this institute are given in NEUMANN's book, "Brotgetreide und Brot" (1st ed., 1914; 3rd ed., 1929).

Italy.— In Italy nearly 5,000,000 ha. are devoted to wheat culture. There is a diversity of conditions associated with mountainous relief and elongated geographic area, resulting in a variety of climates, and as a consequence the region is characterized by a great diversity of species and varieties of wheat. In the enumeration of Prof. DE CILLIS (1927), 96 varieties are listed as having agricultural significance and occupying a considerable area.

For no other area do we have such detailed investigations of the adaptability of varieties to conditions as in Italy. The work of AZZI, "Il clima del grano in Italia" (1922), gives a detailed characterization of the whole region in relation to the conditions of wheat culture and varieties. The physiographic maps furnished by AZZI consider climatic conditions as related to the distribution of varieties, with the favorable and unfavorable factors for each variety. This presents to the breeder the concrete problem of improving varieties for definite regions.

The detailed work of DE CILLIS brings out the characteristics and geography of the varieties and the conditions of wheat culture (1927).

In the northern regions of Italy soft wheat is principally cultivated, while hard wheat is grown in the south; in the moist mountainous regions *T. turgidum* is grown. The local varieties are very diverse, and have interest for us because they include highly productive forms.

During the past two decades, breeding in Italy has been principally associated with the names of two outstanding Italian breeders, TODARO and STRAMPELLI. The former worked principally by individual selection from local populations, the second used the method of hybridization. These are, so to speak, the antipodes of breeding. TODARO is chief of the Institute of Breeding at Bologna, while STRAMPELLI directs the Institute of Genetics in Rome, with an associated institute at Rieti. This institute has its own breeding station. In all Latin countries, the term "breeding" is rendered by the word "genetics," and hence many breeding institutions are called institutions of genetics (in Spain, Mexico, and South America).

The school of TODARO considers that the Italian local wheat populations are very rich in potentialities and one only needs to select from them valuable forms. The school of STRAMPELLI considers that new forms must be created. Both TODARO and STRAMPELLI have produced a number of valuable varieties which, at present, occupy a considerable proportion of the wheat acreage in Italy.

We have already mentioned the important variety "Arditò" developed by STRAMPELLI, and formed by a complex hybridization involving "Dutch Queen Wilhelmina," the local Italian variety "Rieti," and the Japanese variety "Akagomughi." Ardito is particularly valuable for its stiff, short straw, earliness, and yield; it does especially well on fertile soil; its defect is shattering of the grain.

STRAMPELLI produced from the same cross a number of other varieties such

as "Dante," "Fausto Sestini," and "Mentana." By crossing the varieties Rieti × Massy, he produced the well-known varieties "Carlotta Strampelli" and "Varonne." Today in Italy the non-shattering variety "Mentana" is widely grown.

As may be seen, there took part in the creation of these improved hybrid varieties the old local variety "Rieti," which is noteworthy for its universality, being widely distributed in northern Italy and one of the most plastic varieties in its adaptation to different conditions, one of the most productive European varieties, "Wilhelmina" (Holland), and the Japanese early, low-growing variety "Akagomughi."

Todaro developed the varieties "Inallettabile 96," "Gentil Rosso 58," "Gentil Rosso-Semiaristato 48," "Rieti 11," "Cologna 12," "Cologna 31," and others. Recently the Bologna institute has also turned to hybridization.

From the beginning, breeding in Italy has been concerned with soft wheats. Varieties of English wheats (*T. turgidum*) are represented in Italy almost exclusively by local populations.

France.— Until recent times the seed firm Vilmorin et Andrieux had almost a monopoly of wheat breeding in all of France, and also produced varieties for the French colonies. The Vilmorin firm has existed for more than two hundred years, and long ago it became interested in breeding with use of scientific methods. The proprietors of the firm, Louis Levêque, Henri, and Philippe Vilmorin have done much for the science of breeding: they were the first to use pure lines in practice and to work out the methods of breeding with cross-pollinated plants, and in 1873 they began extensive hybridization work with wheat. Louis Levêque De Vilmorin may with justice be considered a founder of the science of breeding. He was the first to make deliberate use of the principle of individual selection in the 50's of the last century. Henri Vilmorin published a comprehensive description of varieties.

Of the 5,500,000 ha. devoted to wheat in France, a considerable part is occupied by varieties developed by the Vilmorin firm.

The Vilmorin breeders produced by complex hybridization many varieties of soft winter wheat (see pedigrees given in the chapter on selection of parents) that are most important. Vilmorin 23 (var. *lutescens*) despite its unattractive head, is distinguished by its excellent grain with good bread-baking quality and its high productivity. A new variety, Vilmorin 27 (var. *lutescens*), produced in 1927, is distinguished by its resistance to lodging.

Of the older varieties we must mention "Dattel" (var. *alborubrum*) which is adapted to northern regions due to its winter resistance, "Bon Fermier" var. *lutescens*) which is distinguished by its yield and good baking quality, and "Hâtif inversable" (var. *lutescens*) which has compact heads, is very resistant to lodging as we may see by its name, and responds well to soil fertilization.

Finally we must mention the superior French spring wheat variety "Aurore" (var. *lutescens*), which was developed by Farrer in Australia by crossing Jacinth × Ladoga, and was then further bred by Vilmorin. This high-yielding, early-maturing wheat is particularly adapted to fertilized soil. A part of the breeding work of the Vilmorin firm was carried out in different parts of France with experiment stations in Tarn, Colmar, and others.

Besides the Vilmorin firm in France there are other private breeding stations of a commercial character. Breeding in France may be regarded as a very profitable undertaking. Quite recently there was established the great agronomic experimental center in Versailles with a breeding section directed by Dr. Shreibe. The work of the Agronomic Institute in Versailles is mainly

of a methodological character; particularly interesting work has been done on winter-hardiness and chemical composition. The institute is well-equipped.

L. BLARINGHEM has worked in France on the genetics of interspecific hybridization.

Poland.— The first handbook on plant breeding in the Russian language was written by the director of the Polish agricultural experiment station, SEMPOLOVSKI: it was published in Petrograd.[96] In this book the author describes the pioneer wheat breeding in Poland beginning with the improvement of local varieties by HALLETT's methods in the second half of the 19th Century (A. YANASH in Dankova, Warsaw Province, V. PEPLOVSKI in Sarny, Plotski Province, K. BELEVSKI in Visokolitovsk, Grodnenski Province, and G. MAZURKEVICH in Nedrzhvitse-Kostelna, Lublin Province).

A. YANASH and SEMPOLOVSKI (at the Sobeshinsk Station) in the 80's of the last century undertook crossing of squareheads with the local varieties "Pulavka" and "Sandomirka."

We must note that a number of winter-resistant and high-yielding old wheat varieties of Poland such as "Pulavka," "Sandomirka," "Banatka," and "Teiskaya" (the last two of Hungarian origin) were introduced into our region from Poland and served as the basis for development, by individual selection, of our best improved varieties of winter wheat such as "2411," "2453," "27," "Ukrainka," and others.

At the present time, practical wheat breeding is carried on in Poland in a number of experiment stations, both by the method of individual selection and by crossing. In 1933 the total wheat acreage in Poland was 1,700,000 ha.

In the National Institute of Agricultural Economy at Pulava there have been rather extensive investigations on the genetics of agricultural characters such as winter-resistance and non-lodging (S. LEWICKI). The results of these investigations have been published in the "Memoirs of the Institute of Genetics" (Pamiętnik Panstwowego Instytutu Naukowego Gospodarstwa Wiejskiego w Pulawach). The genetic investigations of the past two decades, particularly on interspecific hybridization of wheat, have been concentrated in Poland in the Institute of Genetics at the agricultural college in Warsaw under the directorship of Professor E. MALINOVSKI (E. KANEWSKI, W. ARCISZEWSKI, and others). They have published in the "Memoirs of the Genetics Institute" (Pamiętnik zakladu Genetycznego).

Bulgaria.— Breeding work with wheat began here 40 years ago at the experiment station in Obraztsov Chiflik near Russe, in northeastern Bulgaria. Here breeding has been developed by I. IVANOV using individual selection to produce a number of winter wheat varieties. Among them the most widely grown is No. 16 (*Triticum vulgare ferrugineum*). The most resistant to cold are the varieties No. 7 and No. 14 (also *T. vulgare ferrugineum*). In yield, however, these two varieties do not equal No. 16. By crossing No. 16 with the French wheat "Noé," IVANOV developed No. 159. This form is the most productive in Bulgaria, and is distinguished at the same time by its stiff straw and early maturity, although it does not equal No. 16 in winter hardiness.

At the present time wheat breeding at this station is carried on by PROYTCHOFF. In southern Bulgaria, at the station in Sadova, hard and soft wheats are being developed principally by means of individual selection.

Breeding work is also being done in Sofia at the agricultural experiment station and in northern Bulgaria in Knezhe. Here have been developed a number of high-yielding and rust-resistant varieties by the breeder CHOLAKOV.

In addition, there has been significant work in hard wheat breeding by

[96] "Handbook of Seed Breeding and Improvement of Cultivated Plants," 1897.

ANTONOV in southeastern Bulgaria at the station in Chirpan. A limited amount of breeding has also been accomplished in Sofia University by Professor IVANOV. Here are conducted experiments in the testing of milling and baking properties of Bulgarian wheats.

The results of wheat breeding have been published principally in the journal "Svedeniya po Zemledelieto" issued by the Ministry of Commerce and Agriculture in Sofia.[97]

The cultivation of wheat in this country in 1933 embraced 1,235,000 ha.

Rumania.— Here wheat occupied 3,117,000 ha. in 1933. The organized scientific breeding in this region goes back to 1900 when V. C. MUNTEANU, who at that time was director and professor of the Central Agriculural School in Herastrau, began wheat improvement by individual selection from local varieties. In 1911 wheat breeding in the governmental estate in Spantzov began under the directorship of IONESCU-SISESTI, by hybridizing squareheads with local varieties. In this way there were developed early-maturing, rust-resistant, and non-lodging varieties (for example by crossing the variety Balan Laza × Squarehead Hohenheim). In 1913 SANDU-ALDEA in Herastrau began wheat breeding using both the method of individual selection and that of crossing. In the same year there was organized the National Agricultural Association, with the purpose of improving cereal varieties. They invited for consultation the celebrated Swedish breeder NILSSON-EHLE to assist in working out the Rumanian program of wheat breeding. Basic points of this program were:

1. Study of local and foreign wheat varieties;
2. Individual selection from local wheat populations;
3. Crossing local wheat varieties among themselves;
4. Individual selection from foreign wheat varieties;
5. Crossing Rumanian wheat varieties with the best foreign breeding varieties.

The local varieties of Rumanian wheat, as NILSSON-EHLE determined, were comparatively uniform, consisting principally of awned winter types similar to Banatka but having a tendency to lodging and rust-infection.

The wheat breeding program planned by NILSSON-EHLE was carried out by the breeders BASTAKI and ASBIOVICHI.

At the present time wheat breeding in Rumania is carried on partly by private breeders and partly by governmental stations. Of the private firms should be mentioned SAMANTA in Cenad, TIGANESTI (Ilfov), ODOVOS (Arad), FELDIORA (Brazov), and BOD (Brazov). The TIGANESTI and BOD establishments are breeding improving wheat both by individual selection and by crossing. Hybridization, to a less extent, is practiced by the other seed firms.

Recently there have been founded three breeding institutions, in Valakhia, Semigradia, and Moldavia. These three breeding establishments are organized and equipped in accordance with modern European science. In addition, there is a special institute for studying milling and baking qualities of cereal varieties.

Hungary.— The area occupied by wheat in Hungary reaches 1,600,000 ha. Until 1909 wheat breeding in Hungary was being done by private firms, principally by use of mass and individual selection. In this year was founded the governmental breeding institute Magyaròvàr with Dr. E. GRABNER at its head, whose name we associate with the beginning of scientific breeding of wheat in Hungary. Of the private firms the best known is that of ELEMIR SZÈKOIS, whose varieties are still being widely grown in all of Hungary.

Hungary principally cultivates winter wheat, mostly awned forms of the type of "Banatka" and "Teisk" wheats.

[97] Information on breeding in Bulgaria was kindly furnished us by Dr. DONCHO KOSTOV.

The populations of these local varieties have winter-hardiness, drought resistance, and good grain quality. Their undesirable characters include a tendency to lodging, low productivity in comparison with the western European awnless wheats, and attack by leaf rust. These varieties are principally of the subspecies *erythrospermum* and less frequently *ferrugineum*. Of the awnless varieties in Hungary, most widely grown are the wheats Diozzeger and Somogyer which have high productivity but grain of comparatively low quality.

The breeding institute in Magyaróvár is the central directive breeding establishment in the system of the Ministry of Agriculture. In recent years it has made extensive use of hybridization for improving the local wheat varieties. For studying the milling and baking properties there has been created a special laboratory headed by Dr. Hancoszy.

Spain.— Wheat in Spain occupies 4,500,000 ha. Despite the importance of this crop, it occurs principally as local varieties which often are complex populations. In 1927, in our investigations of the Spanish wheats, we collected a large number of forms representing 150 botanical varieties. Such great diversity is associated with the antiquity of the culture in this region, with its nearness to the place of origin of the 28-chromosome species, and with the exceptional range of conditions. In Spain soft wheats, hard wheats, and English wheats (*T. turgidum*) are all cultivated in considerable quantity. In the mountains of Asturia true spelt is grown to considerable extent; the Basques in the Pyrenees even now grow emmers on a sizable acreage; in La Mancha there may still be found a few thousand hectares of einkorn used principally for fattening swine. There is a particularly rich diversity of the Spanish hard and English wheats; the latter are mainly adapted to the moister regions and there is a rich concentration of them in Portugal.

The hard and English wheats have large productive heads with large grain. According to investigations in SSSR, these forms are distinguished by their high resistance to leaf and stripe rusts.

At the beginning of the 19th Century the wheats in Spain were subjected to detailed botanical investigation by the botanist La Gasca, whose excellent wheat herbarium is still preserved in the Madrid Botanical Garden. In this herbarium we can see from La Gasca's own notes that even at this time the strains had been divided into races distinguished within the limits of botanical subspecies.

Wheat breeding is carried on in a limited fashion by a few private firms and also at the agricultural experiment stations near Madrid and in Valladolid.

A description of the wheat varieties grown in Spain at present is given in the book by Azzi, "Le Climat du Blé dans le Monde," Rome, 1930.

Portugal.— Breeding work here is done in the experiment station in Belém, near Lisbon (Estação de ensaio de sementes e melhoramento das plantas). The method of individual selection is used principally. The local wheats are quite diverse, corresponding with the diversity of conditions. Here are grown *T. durum, T. vulgare, T. turgidum,* and *T. polonicum*. The forms of *T. turgidum* and *T. durum* are particularly varied. In the number of varieties of *T. turgidum mediterraneum* Portugal probably occupies one of the foremost places.

Holland.— The total area under wheat cultivation here is not large, about 60,000 ha. The wheat breeding is concentrated in the Institute for Plant Breeding in Wageningen. The greatest accomplishment of Dutch wheat breeding is the variety "Queen Wilhelmina" obtained as a result of crossing an English squarehead with a local Dutch soft winter wheat. The creation of this variety is associated with the name of the Dutch breeder Broekema. This

variety, which was developed at the beginning of this century, during 20 years has not been surpassed by new varieties in yield or other desirable qualities.

Belgium.— Breeding of wheat here is concentrated in Gembloux at the breeding station established in 1913 and directed by C. Journée and V. Lathouwers, authors of one of the best handbooks on plant breeding.

The wheat improvement has been by selection from local wheats and by hybridization. The work has been done mainly with soft winter wheats and with true spelt (*T. spelta*). Hybrids obtained by crossing spelt with soft wheat have been more winter-resistant than the wheat and have had better grain quality.

The objectives of breeding in Belgium are: productivity; early maturity; resistance to lodging, low temperatures, rust, and smut; and the creation of varieties which are adapted to sandy soils and do not sprout excessively from the base.

A minor amount of work is also done with spring wheats.

Sweden.— The history of European breeding of the past decades has been associated with the name of the Swedish breeding station in Svalöf, which has accomplished the most original and fundamental methodological investigations, and at the same time given results of much practical significance. Svalöf, located in southern Sweden in the center of Swedish wheat culture, has rightly been considered the Mecca of breeding science. During 50 years Svalöf has carried on systematic scientific breeding, has uninterruptedly perfected methods, and has brought new materials into the work. The 50 years of breeding in Svalöf is admirably documented and associated with the names of the most competent breeders of the last decades. We recall Neergaard who mechanized breeding by the invention of many devices necessary for the numerical evaluation of varieties. The following director of the Svalöf Station, Nilsen, introduced the method of individual selection used by Louis Vilmorin in France in the first half of the 19th Century. A number of varieties produced by the Svalöf method of individual selection, for example, the "Pobeda" oat, have not been surpassed by world breeding.

Particular interest in the work of the Svalöf Station attaches to the work of Nilsson-Ehle, beginning with the transition from practical breeding to genetics. On the basis of Mendelism, Nilsson-Ehle turned to an extensive organized program of scientific breeding. A feature of Svalöf is the combination of fundamental theoretical work in the field of genetics with the solution of important practical breeding problems. Characteristic of the breeding work in Sweden, as well as in England, is its association with genetics. In both regions the breeders were outstanding geneticists. Nilsson-Ehle worked out the principle of polymerism which is today basic in practical breeding. The best original works on the methods of wheat breeding for such characters as winter-hardiness, disease resistance, and productivity are those of Nilsson-Ehle. He created one of the best international genetic journals, "Hereditas." At the same time he produced excellent varieties: for southern Sweden, "Extra Squarehead T" (1909) and "Soleil" (1911); for central Sweden, "Caniche" (1910); and for northern Sweden, "Thule" and "0801."

As a result of 30 years of work, Nilsson-Ehle by repeated crossings was able to combine cold-resistance with high yield, obtaining the yield principally from English varieties. The new varieties surpassed the old local wheat forms by 40-50%. As in Germany, according to Nilsson-Ehle's estimate, the wheat yield in Sweden increased from 1881 to 1925 by 60%, approximately ⅓, due to the new improved varieties.

After Biffen in England had shown the possibility of combining high yield

with good quality by creating the variety "Yeoman II," the Svalöf workers, finding this variety lacking in sufficient hardiness for Swedish conditions, set themselves the problem of increasing the quality of Swedish wheat, using for this purpose the new English and other varieties.

At present the work on wheat breeding in Svalöf is under the direction of Dr. ÅKERMAN. Besides breeding for quality, much attention in Svalöf is being paid to the creation of early, productive varieties for new northern regions of wheat culture.

Besides the Svalöf Station and its northern substation, breeding in the south of Sweden is also carried on by the WEIBUL firm, which obtained as its scientific directors the noted geneticist KAJANUS, author of the first review of wheat genetics, and HERIBERT-NILSSON.

The main objectives of Swedish breeding are resistance to rust and lodging, winter resistance, and recently, breeding for grain quality and early maturity combined with adaptability to a wide area and extension to the north.

Finland.— During the past three decades the acreage planted to wheat in Finland has increased eight-fold. Instead of 3-4 million kilograms of wheat, at the beginning of this century, at present it produces on the average no less than 24 million kilograms.

The breeding of wheat in Finland has been done at the breeding station in Tammisto (Dr. SAULI) and at the Central Agricultural Station (Dr. V. PESOLA). Most of the wheat in this region is of winter forms. Soft wheats are cultivated exclusively. A number of the local and improved varieties of Finnish wheat have interest for our northern regions, for example, the spring wheat varieties "Tammi," "02," and "Ruskea" which are distinguished by their early maturity, productivity, and adaptation to moist conditions.

Wheat improvement is by individual selection from the old local varieties and by hybridization, particularly with the Swedish varieties.

The principal objectives of winter wheat breeding are productivity, winter resistance, early maturity, non-lodging, and rust resistance. The most valuable variety of winter wheat for Finland is "Sampo," obtained by crossing the Svalöf "Thule II" with a Finnish local variety, other varieties from this crossing—R-023, R-033, and also a number of pure lines developed from local varieties. The work on breeding for winter resistance has been on a particularly wide scale recently (report from Dr. PESOLA in 1934).

Of the spring varieties of wheat, obtained by hybridizing the Canadian "Marquis" and "Prelude," early local varieties, the Finnish variety "Hankkija," the Swedish "Extra Kolben," and winter wheats, there has been obtained the valuable variety "Sopu," which is distinguished by its productivity, comparative earliness, and non-lodging, and also a number of new varieties—R 014, R 031, R 032, which are resistant to stripe rust. The Australian variety "Aurora" in Finland, as well as with us in the North, is one of the best for yields. The spring varieties "Sopu" and "Touko" have high baking qualities; they were obtained by crossing the local variety "Hankkija" with the Canadian "Marquis." A beginning has been made in crossing spring forms with particularly productive winter varieties (Swedish "Thule II" and others) for the purpose of increasing productivity. A good feature of the work of the Finnish Station is its well-prepared reports.[98] The work of this station has particular interest in connection with the problem of extending the wheat area to the north.

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[98] PESOLA, V. Die Weizenzüchtung der landwirtschaftlichen Versuchsanstalt Finnlands. Abt. für Pflanzenzüchtung und ihre Ergebnisse. Valtion Maatalouskoetoiminnan Julkaisuja No. 43, Helsinki, 1932. With a detailed résumé in German.

Wheat Breeding in Russia:—The beginning of wheat breeding in our land goes back to the work of D. L. RUDZINSKI in 1902, at the Agricultural Academy near Timiryazev (at this time the Agricultural Institute) under the direction of Professor V. R. WILLIAMSON, in the chair of general agriculture. Despite the very modest extent and area of the work, D. L. RUDZINSKI developed by individual selection from Hungarian and Polish wheats excellent winter wheat varieties, such as numbers 2411, 2453, A-27, and 2460, which up to this time appear to be the best Soviet varieties for non-chernozem soils.

In 1908, in the Bureau of Applied Botany of the Scientific Committee of the Ministry of Agriculture, there was developed work on the botanical study of our wheats under the directorship of R. E. REGEL and K. A. FLAKSBERGER. This small institution, on the basis of which there later rose the Pan-Soviet Institute of Plant Industry, first took up the botanical principles of breeding and organized for our region the systematic-geographic study of wheat.

The investigation of the genetic potentialities of wheat during the past decade led to the determination, within the limits of the old world, of the original points of species and variety differentiation. During 1924-1933 the Institute of Plant Industry made a series of systematic investigations of the basic regions of wheat culture, including places of ancient agriculture that had not been studied up to this time, such as Iran, Afghanistan, Turkey, Abyssinia, Syria, Palestine, and others. As a result there was gathered a colossal amount of original varietal material, totalling 31,000 specimens, and these were subjected to detailed botanical-agronomic investigation. There were discovered a number of new species of wheat, and a great number of new subspecies; new varietal characters were found; these investigations first gave a botanical-geographical basis for wheat breeding by determining the regions of concentration of species, varieties, and genes. This was the first basic problem of original materials in wheat breeding.

Simultaneously the Institute of Plant Industry branched out into a systematic many-sided study of the world wheat assortment, using the methods of physiology, biochemistry, genetics, and technology.

The first series of geographic experiments, conducted in 1923-1928, made it possible to determine geographic regularities in variation in the chemical composition of wheat, changes in the vegetative period, and behavior of the different "systematic" characters.

In 1924 there were organized the Pan-Soviet Governmental Variety Tests of the best Soviet and foreign breeding varieties, which grew into a great organization embracing all regions with a network of variety-testing stations. The final evaluation of varieties included the determination of all important agricultural elements, including immunity from diseases, chemical composition, bread-baking and milling qualities, adaptability to mechanical harvesting, etc. On the basis of many years' results, the governmental variety tests led to a planned change of wheat varieties. The results of the work of the governmental network on wheat were published in a number of monographs. For purposes of official approval there were published special detailed descriptions of all tested Soviet and foreign varieties. Recently there have also been published detailed maps on the distribution of the different varieties.[99]

In 1909 there was founded the *Kharkov Breeding Station* which grew into a great breeding center dealing with winter and spring wheats (V. YA. YUREV). Beginning with the method of individual selection and later using hybridization, it produced the winter wheat varieties *"Erythrospermum* 0917," *"Ferrugineum* 01239," *"Albidum* 0676," and *"Milturum* 120." The variety "13/676" has a

[99] Regions of Culture of Cereal Varieties VIR, 1935.

high degree of winter hardiness and is sensitive to fertilization. The Kharkov Station produced the spring wheat varieties "11/502" and "12/50" which are comparatively resistant to attack by the Hessian fly. In spring wheats there has been extensive work using interspecific hybridization.

In 1910 was founded the Saratov Breeding Station which developed extensive work on spring wheat and later also with winter wheat. The first reports on wheat from this station, evaluating the original local and foreign materials and also describing the methods of breeding, still have interest at the present time.

The work of the breeding station in Saratov has been particularly extensive in the past decade under the leadership of Professor G. K. Meister. By individual selection the station developed a number of valuable spring wheats, such as "*Lutescens* 062" and "*Erythrospermum* 0341," a series of hard wheats, (for example "*Gordenforme* 0432"), and a number of winter wheats of which "0329" and "1060/10" (both *lutescens*) appear to be the most winterhardy Soviet wheats. "*Hostianum* 0237" also is a valuable variety.

In the past decade the work of the Saratov Station has been concentrated primarily on interspecific and intergeneric hybridization, the results of which have been given in the chapter on this subject. Among the greatest practical accomplishments of the station we may note the awnless hybrid between hard and soft wheats, "Sarrubra," obtained by crossing "Poltavka" and "Beloturki." This hybrid today occupies hundreds of thousands of hectares in cultivation, and appears to be the greatest practical accomplishment in the world in interspecific hybridization of wheat.

It is impossible not to call attention to the very valuable investigations on the physiology of wheat varieties, particularly in relation to drought resistance and winter hardiness, carried out at the station by V. R. Zalenskii, A. A. Rikhter, and others.

We note in addition the important work of the *Odessa Breeding Station,* today known as the *Genetics-Breeding Institute.* This station, under the directorship of A. A. Sapehin, has produced by individual selection from local varieties and Hungarian Banatok wheat, the winter wheats "Cooperatorka," "Stepnyachka," and "Zemka." Distinguished by their high drought resistance, grain quality, and productivity, these wheats unfortunately have insufficient winter-hardiness, particularly the latter two. Here has begun extensive interspecific hybridization of hard and soft wheats based on modern methods of cytogenetics.

For purposes of practical breeding, hybridization has been carried out on a very great scale, with several hundreds of thousands of plants in the F_2 and F_3 generations.

For evaluating the varieties with respect to winter-hardiness and drought resistance, there have been introduced the present-day methods of physiology, with the use of cold and drought chambers. Here there has been interesting work on breeding for immunity from Swedish and Hessian flies and from rust.

In a methodological respect the work of the Odessa Station is outstanding in Soviet wheat breeding.

At the present time the Genetics-Breeding Institute in Odessa is conducting much original work in vernalization of wheat and using this to aid in crossing (T. D. Lisenko). These investigations have unusual interest, disclosing new horizons to the wheat breeder, particularly from the standpoint of using the study of development by stages for selecting the original parental forms.

Of the *Ukrainian* institutions we note the work of Mironovski at the

Sugar Trust Station in developing the winter wheat "Ukrainka" from the Hungarian "Banatka" (breeding of I. M. Eremeeva). This variety today is widely distributed throughout the regions of Southern Ukraine and North Caucasus. Probably no less than half of all the winter wheat in SSSR at present is "Ukrainka," which is distinguished by its high productivity, its good milling and baking quality, and its universal adaptation.

The *Ivanovsk Station* (Kharkov region) has produced the winterhardy variety "Durable" (*"Erythrospermum* 0348") which today occupies a significant territory both in Ukraine and in the non-chernozem strip of the European part of the Union. It was derived from the Hungarian "Banatka" by individual selection, and is distinguished by its exceptional universality, extending in culture northward to the Leningrad region.

We also note a series of varieties of winter wheat developed by the Sugar Trust Station, "0351" of the *Verkhnyachsk Station,* No. 7 and No. 11 of the *Veselo-Podolyansk Station,* and "2537-64," of the *Nemerchansk Station.*

The *Dnepropetrovsk Station* (V. V. Talanov) has produced the hard wheats *"Hordeiforme* 010" and *"Melanopus* 037."

The *Crimean Station* (Simferopol), from the local winter wheat "Krimka," by individual selection, derived "Novokrimka" which is noted for its drought resistance, earliness, and high quality grain. According to the data of the variety tests, this variety may also be used in the steppe regions of Ukraine.

In *North Caucasus* significant work on breeding has been done at the Kubansk Station ("Kruglik") and the Stavropol Station. The *Kubansk Station* has produced the high-yielding variety of hard wheat "Hordeiforme 027" and the productive winter varieties "Sedouska 0392" and "0393." Particularly interesting are new winter varieties that are resistant to leaf rust and today are being increased at the station.

The *Stavropol Station* has produced, by means of individual selection, the winter wheats "455" and "622" and also a number of spring hard and soft wheats.

From the *Volga Breeding Institute,* besides that at the above-mentioned Saratov Breeding Station, considerable breeding work is also done at the Krasnokutsk, Bezenchuksk, and Kazansk Stations.

The *Krasnokutsk* and *Bezenchuksk Stations,* by individual selection from local varieties, have produced excellent drought-resistant soft and hard spring wheats (*Erythrospermum* 0841, *Graecum* 01774—of the Khikinka type, *Hordeiforme* 0189, and the universal *Melanopus* 069). The *Bezenchuksk Station* has conducted considerable hybridization work for the purpose of obtaining winter-resistant winter wheats.

The *Verkhnevolzhsk* (*Kazansk*) *Station* has produced by selection the variety of winter wheat No. 16 (*erythrospermum*), which is distinguished in its region of adaptation by drought resistance and winter resistance.

The *Simbileevsk Station* (Gorkovsk Region), organized in 1921, has developed by individual selection the winter-resistant winter wheat varieties "146" and "134" which have good baking qualities.

The *Kirovsk* (*Vyatsk*) *Breeding Station* (N. V. Rudintskii), by individual selection, has developed varieties of spring (No. 32, No. 26) and winter (No. 4, No. 5) wheats. As shown by the data of the governmental variety tests, these varieties have particular interest for the non-chernozem soil strips.

The *Shatilovsk Station* has produced (T. I. Lisitsin) the winter wheat "0409," and recently has expanded into considerable hybridization work, crossing hard wheats with emmers and making other combinations to produce varieties with resistance to attack of the Swedish fly.

The *Detski Village Station* of the Institute of Plant Industry (V. E. PISAREV) by hybridization has created the early maturing variety of spring wheat "Novinka" (V. E. PISAREV), for obtaining which a Canadian variety was used. A number of valuable hybrids of spring wheats are in the process of testing at the present time. This station has recently done extensive breeding work with winter wheats.

In *Siberia* we note the work of the Omsk, Krasnoyarsk, and Tulinsk Stations.

The *Omsk Station,* opened in 1912, began, under the leadership of N. L. SKALOZUBOV, a broad program of breeding work with spring wheats. Later work of the station (V. V. TALANOV) developed the excellent spring wheat varieties *"Caesium* 0111," which is very plastic and today occupies millions of hectares, and *"Milturum* 0321." These varieties were produced by selection from local and foreign wheats through the careful investigations of TERNOVSKI.

At present there is particular interest at this station in the hybridization of wheat with *Agropyrum* (N. V. TSITSIN) as discussed above.

Extensive breeding work has been done on spring wheats at the *Tulinsk Station* in western Siberia, under the leadership of V. E. PISAREV. This station, in 1915, began the general use of intraspecific hybridization. On the basis of the hybrids produced there developed the further work of the breeding station in Detski Village.

The investigations of local wheat varieties carried on at the Tulinsk Station represent one of the best examples of a many-sided, detailed study of local varieties. By means of individual selection, the station isolated from the local old western Siberian wheats the variety "Balaganka" or "Tulun 81/4," distinguished by its resistance to the spring fly which is common in a number of east Siberian regions.

The *Krasnoyarsk Station* in eastern Siberia has produced a number of early maturing varieties of spring wheats including "Leda."

The *Amur Station* near Blagoveshchensk (V. A. ZOLOTNITSKI) has developed a number of valuable pure lines of spring wheat. Of the varieties suitable for the Far East, mention should be made of "Strube," a product of German breeding which is interesting for its resistance to fungus diseases.

Finally, for *Central Asia* we must mention the results of breeding at the *Krasnovodopadsk Station* near Tashkent (A. K. GOLBEK), where from local populations have been selected a number of highly productive and drought-resistant varieties of soft wheats suited to local conditions.

Detailed investigations of wheat in Central Asia and Kazakstan have been made by V. K. KOBELEV (in press).

* * * * *

Considering the conditions of a rigorous continental climate, practical breeders in the Soviet Union have naturally directed their attention to such characters as drought resistance, winterhardiness, early maturity, and, recently, grain quality and immunity from diseases. A majority of the new varieties have been obtained by individual selection from local or foreign populations. Many of our best winter varieties have been derived from Hungarian and Polish winterhardy wheats. Thus the Hungarian "Banatka" was the origin of such improved varieties as "Ukrainka," "Moskovskaya 02411," "Durable," "Stepnyachka," and others. "Banatka" itself was brought from Hungary and has become widely distributed throughout the Ukraine and surrounding areas. The Polish "Sandomirka" served as the original population from which was derived the variety *"Lutescens* 0329" of the Saratov Station, which is record

breaking in its winterhardiness. Spring varieties of hard and soft wheats have also been derived principally from local populations.

Only in the past decade has much attention been given to crosses. In use of distant hybridizations and the extent and originality of its undertakings Soviet wheat breeding is internationally outstanding. Despite the short period of the work, Soviet breeding has achieved great accomplishments with both spring and winter wheats, making it possible for us to have a full assortment of seed materials of new bred varieties in the near future.

The problems of Soviet breeding are sufficiently described in the chapter on the ideal wheat variety. There is no doubt that in the future Soviet breeding must proceed principally by hybridization within the limits of species, using combinations of different species and genera.

The breeder must give particular attention to immunity, winterhardiness, drought resistance, non-shattering of the grain, and adaptation to mechanical harvesting, as well as milling and baking quality.

Problems in Future Wheat Breeding:— From all that has been written above, the great problems before Soviet and world breeders may be clearly seen. Modern wheat breeding has only begun: actually it embraces a period no greater than 30 years. Now we know more or less completely the initial species and varietal composition of the world wheat potential and have it. There have been discovered a wealth of species and forms of 28-chromosome wheats unknown to scientific breeders of the past.

The study of growth stages opens up new possibilities in the use of the world resources of wheat varieties. Physiology is approaching an organized evaluation of the world assortment of wheats according to winterhardiness and drought resistance. Biochemistry is going deeply into an analysis of the protein fraction of wheat. The genetic nature of characters in a majority of species still has not been worked out. The great specific and varietal potentials have still been used only to a limited extent in practical breeding. The science of the selection of parental pairs is just beginning to be formulated into concrete theory. Basically, the use of systematic cyclic crosses for combining important characteristics in which the breeder is interested, is needed for determining the most promising practical combinations. A most important problem, although a difficult one, lies in the field of distant hybridization to effect radical changes in the wheat plant.

Scientific breeding must find a way of creating, in a short time, necessary forms which combine, within single varieties suited for different conditions, a maximum number of valuable characters.

In order to achieve a solution of this great problem, we need sound fundamental theory, and we need the combined work of breeders with geneticists, physiologists, chemists, technologists, phytopathologists, and entomologists.

THE LENIN ACADEMY OF AGRICULTURAL SCIENCES
INSTITUTE OF PLANT INDUSTRY

THEORETICAL BASES OF PLANT BREEDING

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GRAIN AND FORRAGE CROPS

Prof. N. I. Vavilov
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Том 2

ЧАСТНАЯ СЕЛЕКЦИЯ
ЗЕРНОВЫХ И КОРМОВЫХ КУЛЬТУР

Под общей редакцией академика
Н. И. Вавилова

ГОСУДАРСТВЕННОЕ ИЗДАТЕЛЬСТВО
СОВХОЗНОЙ И КОЛХОЗНОЙ ЛИТЕРАТУРЫ
МОСКВА • 1935 • ЛЕНИНГРАД

FIGURE 12. — Title pages of the second volume of VAVILOV's 'Theoretical Bases' (1935)

SELECTED BIBLIOGRAPHY OF THE BASIC WORLD LITERATURE ON BREEDING AND GENETICS OF WHEAT

The literature on breeding and genetics of wheat, which is interwoven with the literature on the culture of wheat in general, is very extensive, including thousands of titles. Besides a considerable number of books, it is principally concentrated in the following periodicals:

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See also contributions of the experiment stations, giving information on breeding activities.

ILLUSTRATIONS

of

TRITICUM
SPECIES

and

VARIETIES

Рис. 1. Соматическая ядерная пластинка. Хромосомы в корешках (2n = 28) Triticum durum subsp. abyssinicum var. Schimperi Körn. Аддис-Абеба. № 19074. Препарат и рисунок Г. А. Левитского.

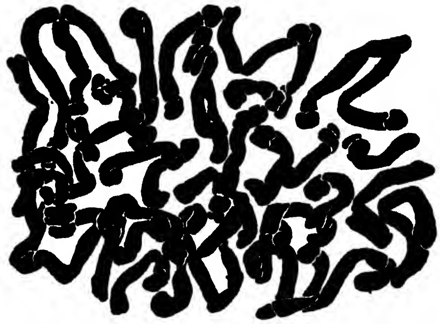


Рис. 2. Соматическая ядерная пластинка. Хромосомы в корешках (2n = 42) Triticum vulgare var. ferrugineum A l., № 19300. Абиссиния. Препарат и рисунок Г. А. Левитского.

FIGURE 13 (FIG. 1, *above*).— Somatic nuclear plate. Chromosomes (2n = 28) of *Triticum durum* subspecies *abyssinicum* var. *schimperi* Körn., Addis Ababa, 19074.

FIGURE 14 (FIG. 2, *above*).— Somatic nuclear plate. Chromosomes (2n = 42) of *Triticum vulgare* var. *ferrugineum* Al., Abyssinia, 19300. Preparation and drawings by G. A. LEVITSKI.

FIGURE 15 (FIG. 3, *at right.*)— *Triticum timopheevi* Zhuk., Timopheevi wheat (28 chromosomes). Determined in West Georgia by Professor P. M. ZHUKOVSKI. Distinguished by its very high resistance to leaf stripe, and stem rust.

FIGURE 16 (FIG. 4, *at right*).— *Triticum sphaerococcum* Perc., Round-grained wheat from northern India discovered by Professor PERCIVAL (42 chromosomes). Drawn by M. P. LOBANOVA.

FIGURE 17 (FIG. 5, *at right*).— *Triticum macha* Dekapr. et Men., Macha wheat. A new wheat species (42 chromosomes) determined by Professor L. L. DEKAPRELEVICH in Western Georgia. Drawn by A. M. SHEPELEVA.

FIGURE 18 (FIG. 6, *at right*).— *Triticum vulgare compositum* var. *vavilovi* Tum. (*T. vaviloviana* Jakubz.) (42 chromosomes). Endemic in Turkish Armenia. Distinguished by its non-shattering and branching. Found and first described by M. G. TUMANYAN near Lake Vana. Drawn by M. P. LOBANOVA.

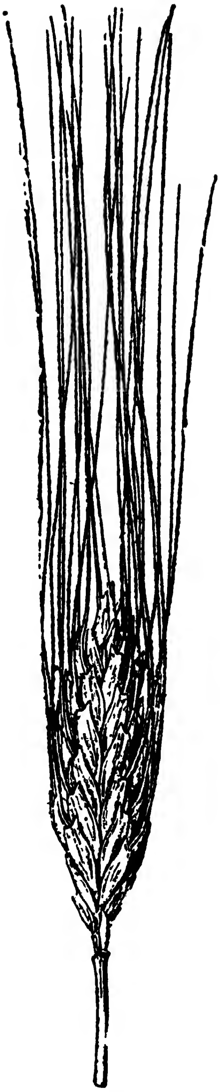


Рис. 3. Triticum Timopheevi Zhuk. — Пшеница Тимофеева (28 хромосом). Установлен в западной Грузии проф. П. М. Жуковским Отличается исключительной устойчивостью к бурой, желтой и стеблевой ржавчинам.

Рис. 4. Triticum sphaerococcum Perc. — Круглозерная пшеница из Сев. Индии, открытая проф. Персивалем (42 хромосомы). Рис. М. П. Лобановой.

Рис. 5. Triticum macha Dekapr. et Men. Пшеница-маха. Новый вид пшеницы (42 хромосомы), установленный проф. Л. Л. Декапрелевичем в западной Грузии. Рис. А М Шепелевой.

Рис. 6. Triticum vulgare compositum var. Vavilovi Tum. (Tr. Vavilovian Jakubz.) (42 хромосомы) — эндемичен для Турецкой Армении. Отличается неосыпаемостью, ветвистостью. Найден и впервые описан проф. М. Г. Туманьяном около оз. Вана. Рис. М. П. Лобановой.

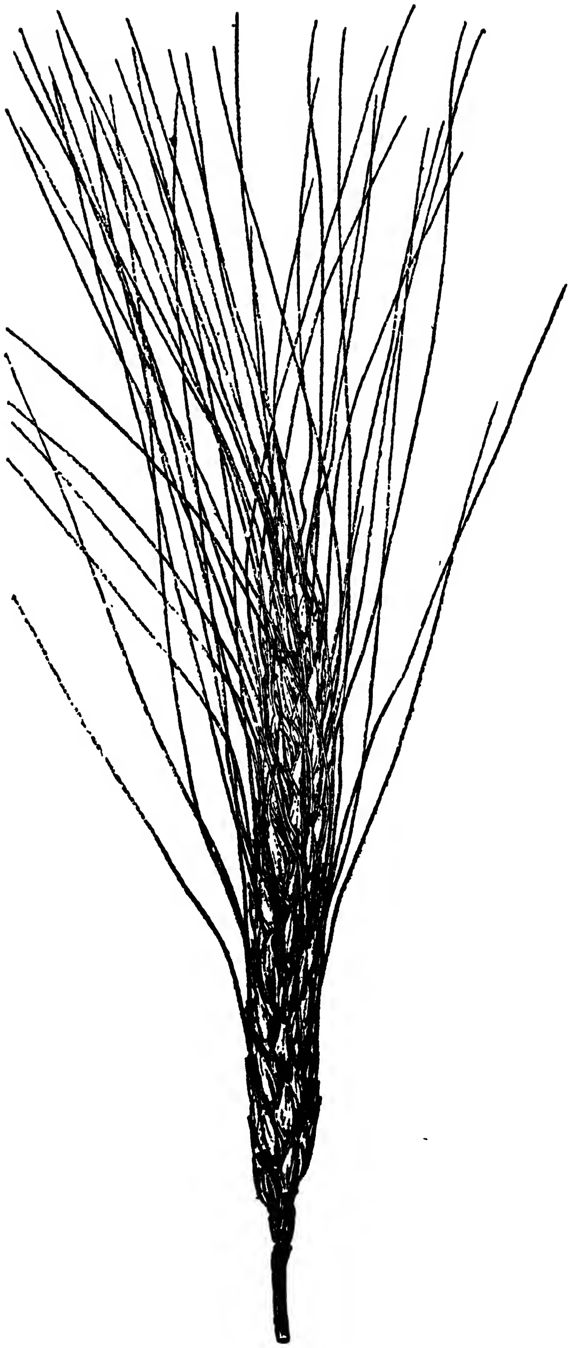


Рис. 7. Triticum durum abyssinicum var. Arraseita Körn subv. aristiforme Абиссиния район Фичи. № 19566. Рис. М. П. Лобановой.

FIGURE 19.—*Triticum durum abyssinicum* var. *arraseita* Körn. subvar. *aristiforme*. Abyssinian region, 19566. Drawn by M. P. LOBANOVA.

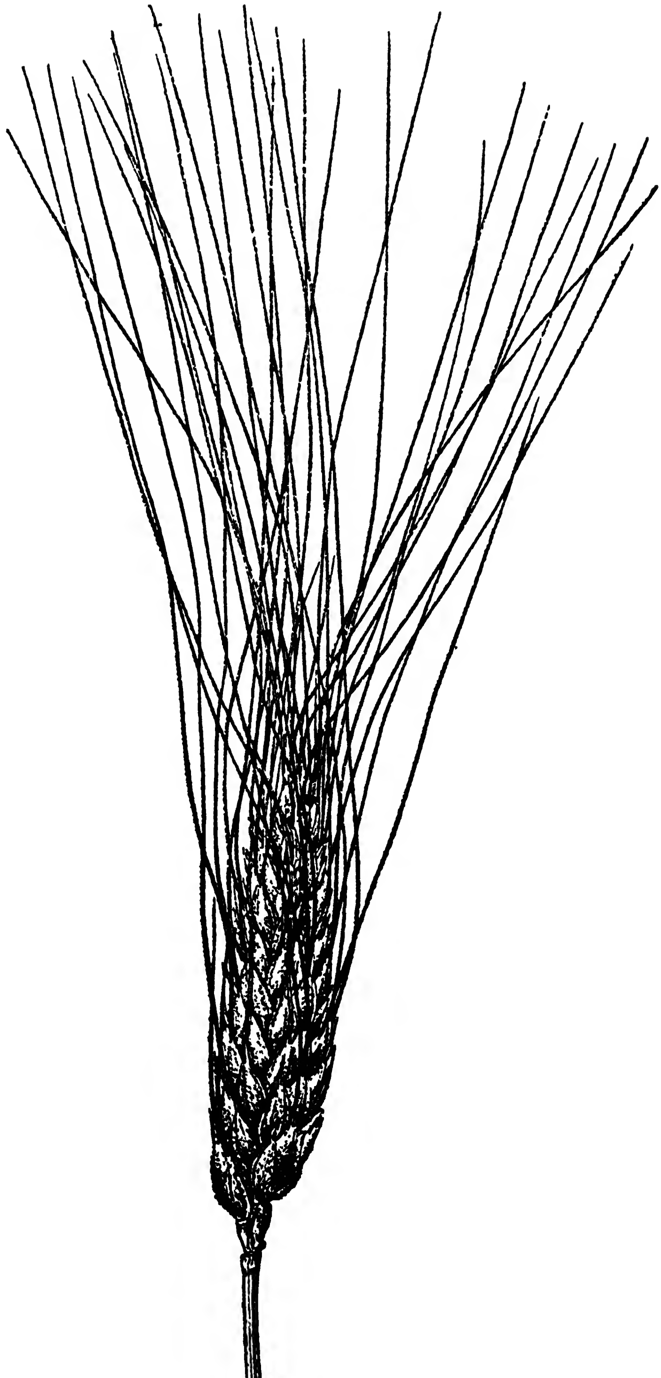


Рис. 8. Triticum durum abyssinicum var. negustianum V a v. subv. aristiforme. № 18996. Абиссиния, район Харрара.

FIGURE 20.— *Triticum durum abyssinicum* var. *negustianum* Vav. subvar. *aristiforme*. Abyssinia, 18996, Kharrara region.

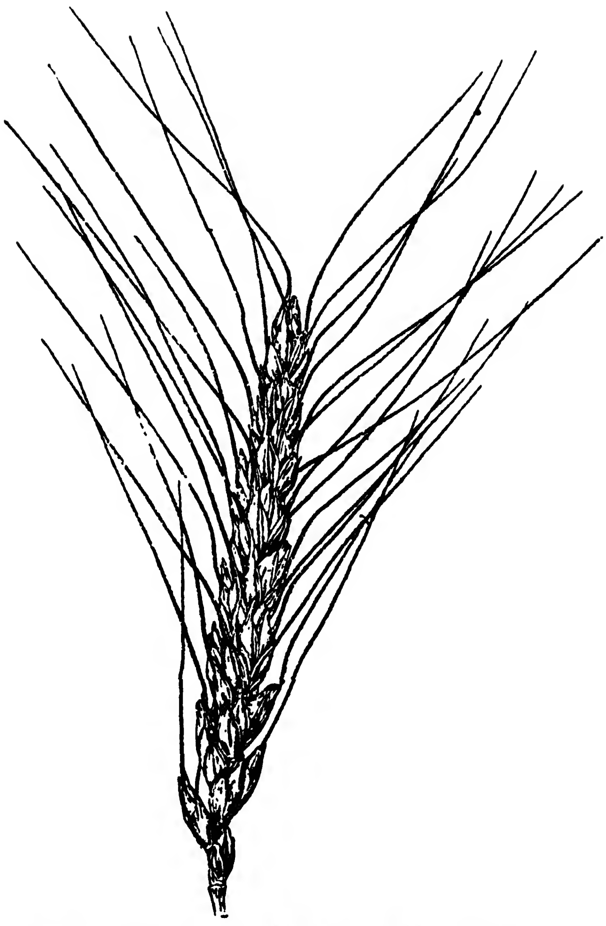


Рис. 9. Triticum turgidum abyssinicum var. atrato-purpureum Vav. (6) subv. brevidentatum. № 19569. Абиссиния, район Фичи. Рис. М. П. Лобановой.

FIGURE 21.— *Triticum turgidum abyssinicum* var. *atrato-purpureum* Vav. (6) subvar. *brevidentatum*. Abyssinia, 19569. Drawn by M. P. LOBANOVA.

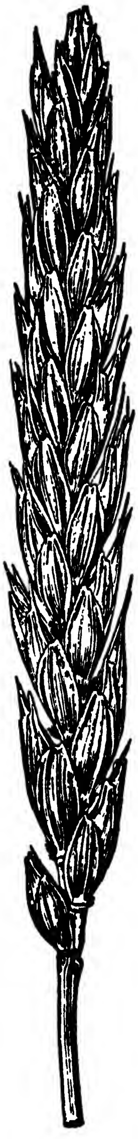


Рис 10. Безостая форма твердой пшеницы Tr. durum abyssinicum var. axumicum Vav. subv. brevidentatum. № 19604. Абиссиния, район Гондара. Рис. М.П. Лобановой.

Рис. 11. Безостая инфлятная раса Triticum turgidum abyssinicum var. rubrinflatum Vav., с резко выраженными лопастями у основания остевидных заострений. Эритрея Асмара. № 19650. Рис. М.П. Лобановой.

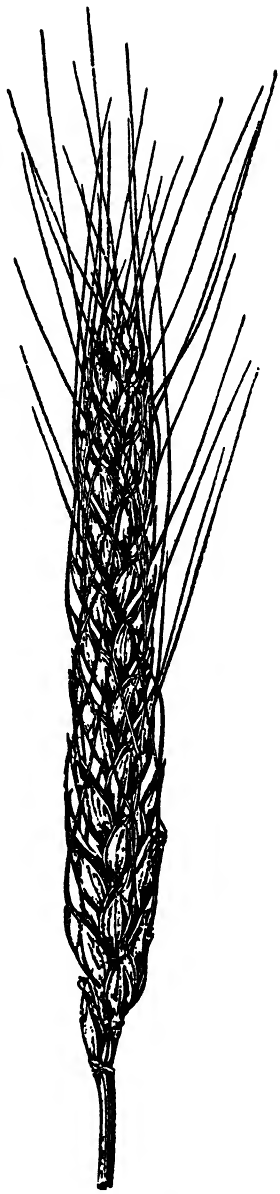


Рис. 12. Triticum turgidum abyssinicum elongatum var. purpureum Vav. subv. brevidentatum. Рыхлоколосая короткоостистая форма Tr. turgidum abyssinicum Абиссиния Аддис-Абеба. № 19286. Рис. М. П. Лобановой.

FIGURE 22.— Awnless form of hard wheat, *T. durum abyssinicum* var. *axumicum* Vav. subvar. *brevidentatum*. Abyssinia, 19604, Gondara region. Drawn by M. P. LOBANOVA.

FIGURE 23.— Awnless inflated race of *Triticum turgidum abyssinicum* var. *rubrinflatum* Vav. with sharply expressed irregularity of the base of the awnlike processes. Eritrea, Asmara, 19650. Drawn by M. P. LOBANOVA.

FIGURE 24.— *Triticum turgidum abyssinicum elongatum* var. *purpureum* Vav. subvariety *brevidentatum*. Loose-headed, short-awned form of *T. turgidum abyssinicum*. Abyssinia, Addis Ababa, 19286. Drawn by M. P. LOBANOVA.

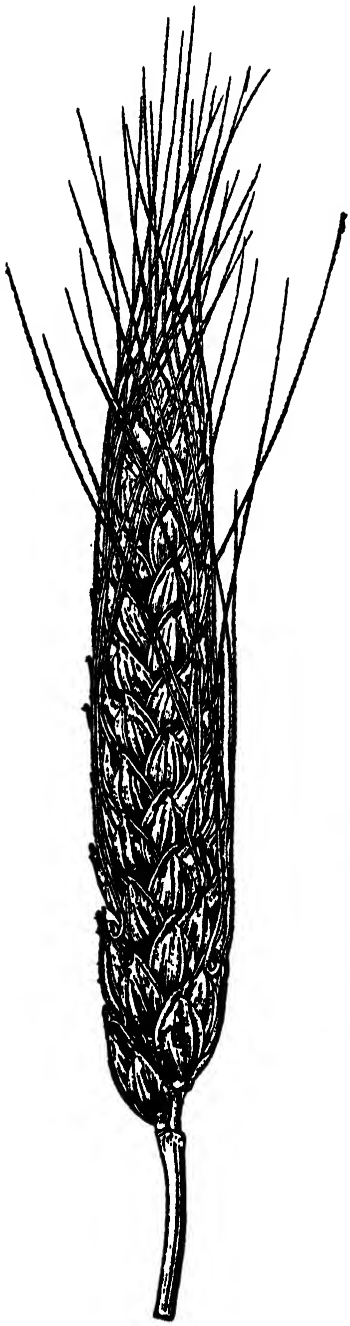


Рис. 13. Triticum turgidum abyssinicum densum var. decoloratum Vav. subv. brevidentatum. Плотноколосая форма. Абиссиния. Аддис - Абеба. № 19244. Рис. М. П. Лобановой.

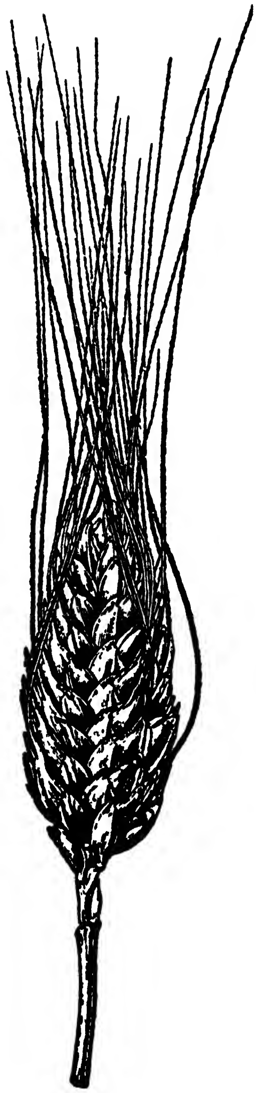


Рис. 14. Triticum turgidum abyssinicum var. rubidicompactum subv. brevidentatum. Форма с очень плотным коротким колосом. Эритрея. Асмара. № 19650. Рис. М. П. Лобановой.

FIGURE 25.— *Triticum turgidum abyssinicum densum* var. *decoloratum* Vav. subvar. *brevidentatum*. Compact-headed form. Abyssinia, Addis Ababa, 19244. Drawn by M. P. LOBANOVA.

FIGURE 26.— *Triticum turgidum abyssinicum* var. *rubidicompactum* subvariety *brevidentatum*. Form with very compact short heads. Eritrea, Asmara, 19650. Drawn by M. P. LOBANOVA.

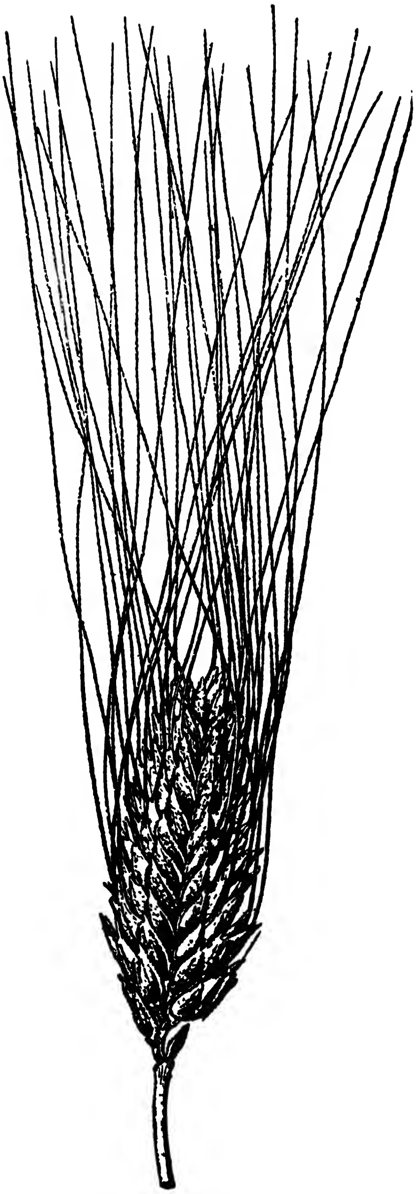


Рис. 15. Triticum durum abyssinicum var. pseudo-copticum Vav. subv. longidentatum. Абиссиния, район Харрара. № 19002. Рис. М. П. Лобановой.

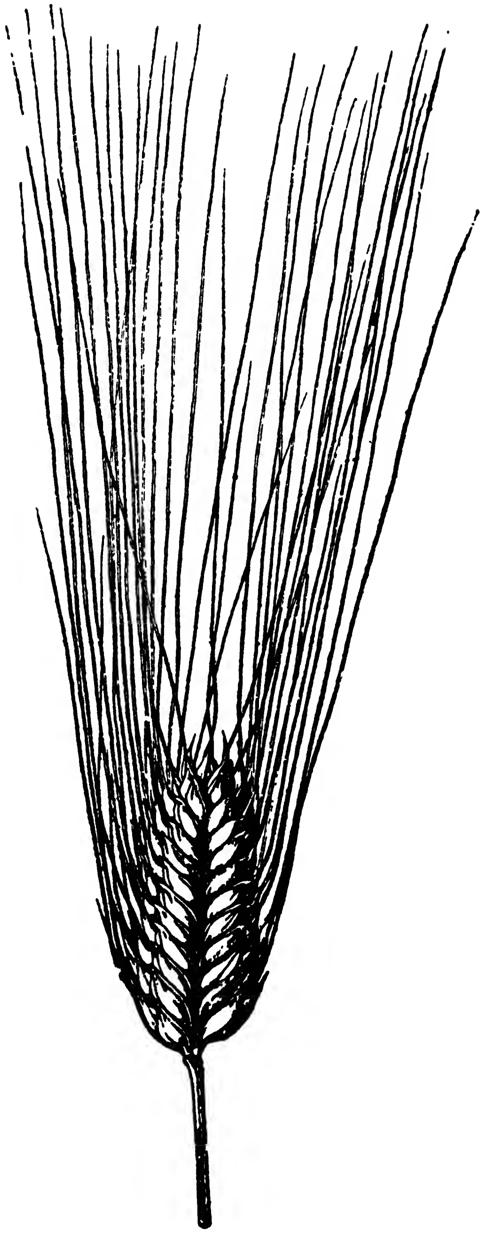


Рис. 17. Triticum durum var. pseudo-leucomelan Vav Марокко. № 16409. Типичный представитель секции africana Vav. Рис. А. М. Шепелевой.

FIGURE 27.— *Triticum durum abyssinicum* var. *pseudo-copticum* Vav. subvar. *longidentatum*. Abyssinia, Kharrara region, 19002. Drawn by M. P. LOBANOVA.

FIGURE 28.— *Triticum durum* var. *pseudo-leucomelan* Vav. Morocco, 16409. A typical representative of the section *africana* Vav. Drawn by A. M. SHEPELEVA.

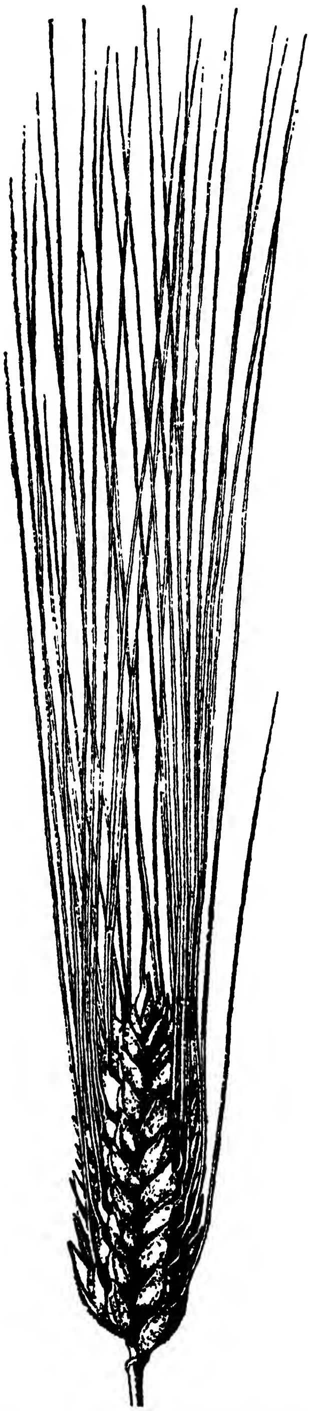


Рис. 18. Triticum durum var. melanopus Al. № 2023. Типичный представитель египетской группы твердых пшениц (egyptiaca). Рис. А. М. Шепелевой.

Рис. 19. Triticum turgidum subsp. mediterraneum Flaksb. var. megalopolitanum. Сицилия. № 20050. Рис. А. М. Шепелевой.

FIGURE 29.— *Triticum durum* var. *melanopus* Al., 2023. Typical representative of Egyptian group of hard wheats (*egyptiaca*). Drawn by A. M. SHEPELEVA.

FIGURE 30.— *Triticum turgidum* subsp. *mediterraneum* Flaksb. var. *megalopolitanum*. Sicily, 20050. Drawn by A. M. SHEPELEVA.

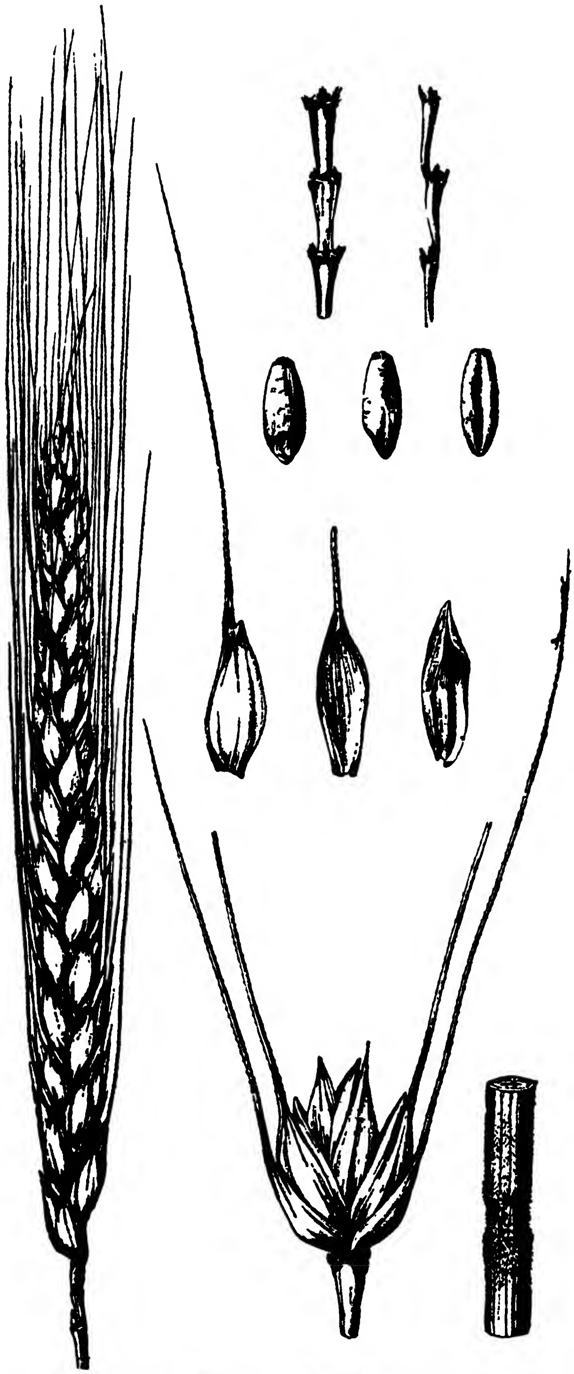


Рис. 20. Triticum persicum Vav. var fuliginosum Zhuk. Персидская пшеница. Распространена в Грузии и Армении.

FIGURE 31.— *Triticum persicum* Vav. var. *fuliginosum* Zhuk. Persian wheat. Distributed in Georgia and Armenia.

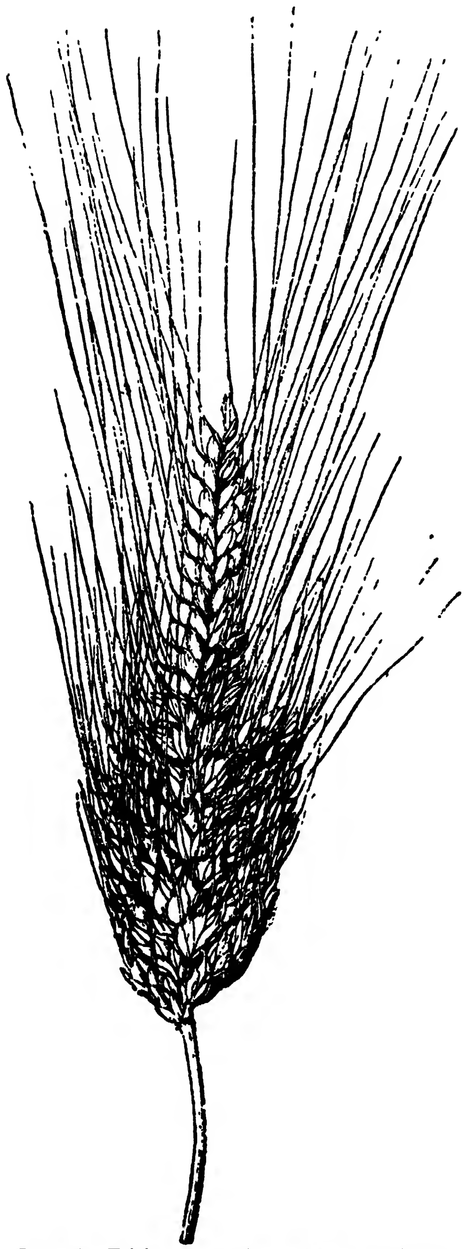


Рис. 22. Triticum turgidum var. pseudo-cervinum Körn. Английская ветвистая пшеница. Португалия. № 20665 Рис. А. М. Шепелевой.

FIGURE 32.—*Triticum turgidum* var. *pseudo-cervinum* Körn. English branched wheat. Portugal, 20665. Drawn by A. M. SHEPELEVA.

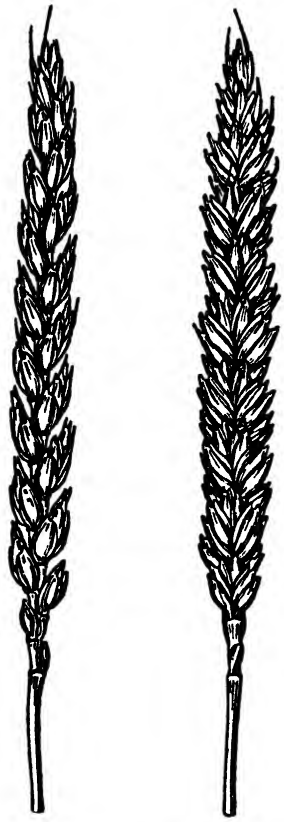


Рис. 37. Канадский сорт «Маркиз». $^1/_1$. Рис. М. П. Лобановой.

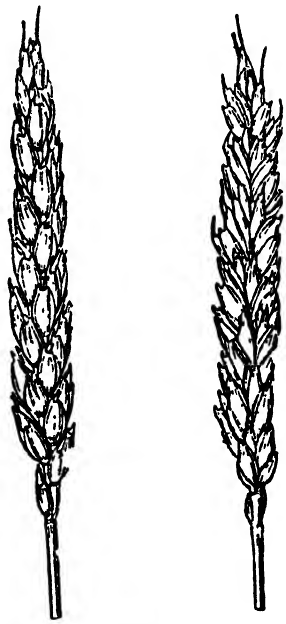


Рис. 38. «Саррубра» — безостый гибрид твердой и мягкой пшеницы, выведенный Саратовской селекционной станцией. $^1/_1$. Рис. М. П. Лобановой.

FIGURE 33.— Canadian variety "Marquis". Drawn by M. P. LOBANOVA.

FIGURE 34.— "Sarrubra", awnless hybrid of hard and soft wheat developed at the Saratov Breeding Station. Drawn by M. P. LOBANOVA.

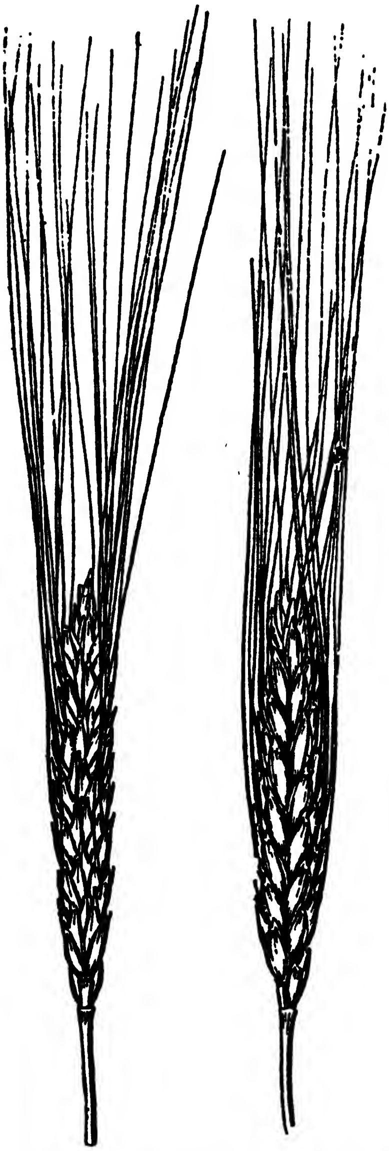


Рис. 39. Твердая пшеница «Гордеиформе 010», выведенная Днепропетровской станцией.

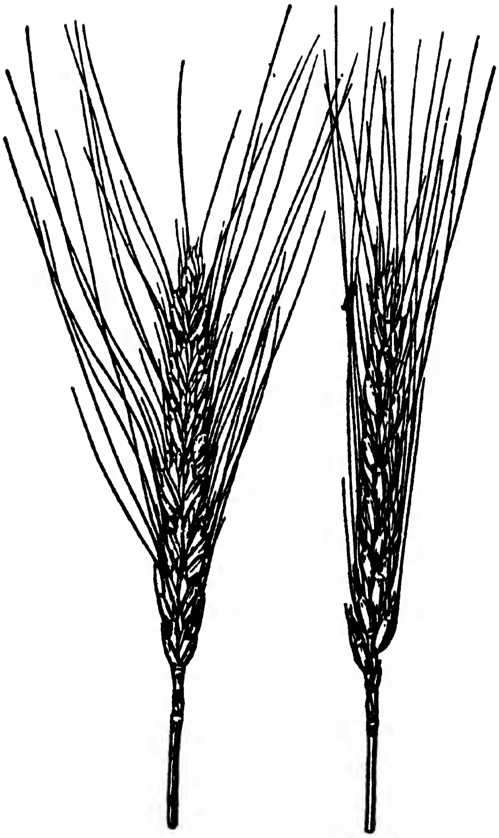


Рис. 41. Яровая пшеница «Цезиум 0111» — один из лучших ярсвых сортов, выведенный Омской с.-х. станцией. $^{3}/_{4}$. Рис. М. П. Лобановой.

FIGURE 35.— Hard wheat "Gordenforme 010" developed by the Dnepropetrovsk Station.

FIGURE 36.— Spring wheat "Caesium 0111", one of the best spring varieties, developed by the Omsk Agricultural Station. Drawn by M. P. LOBANOVA.

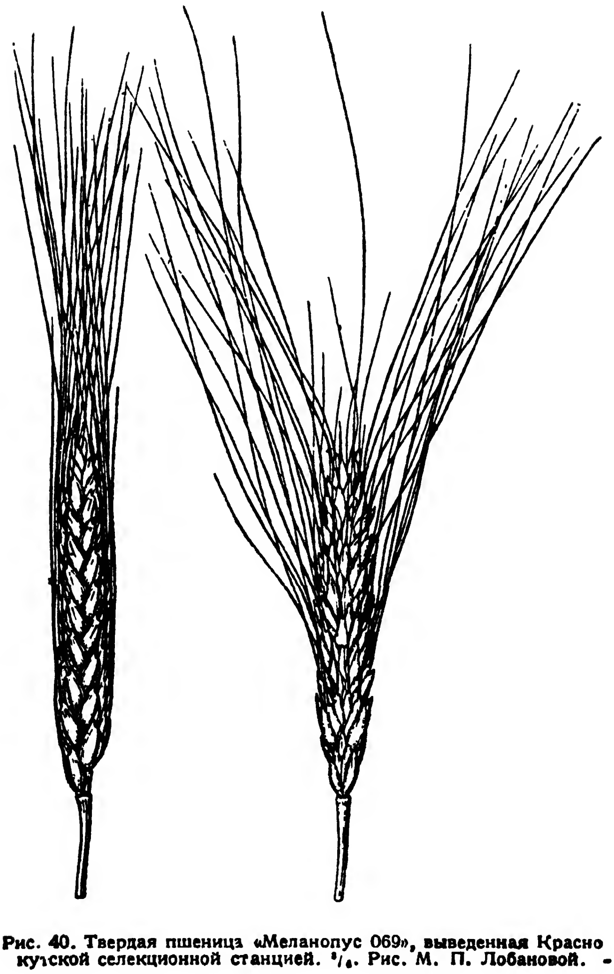
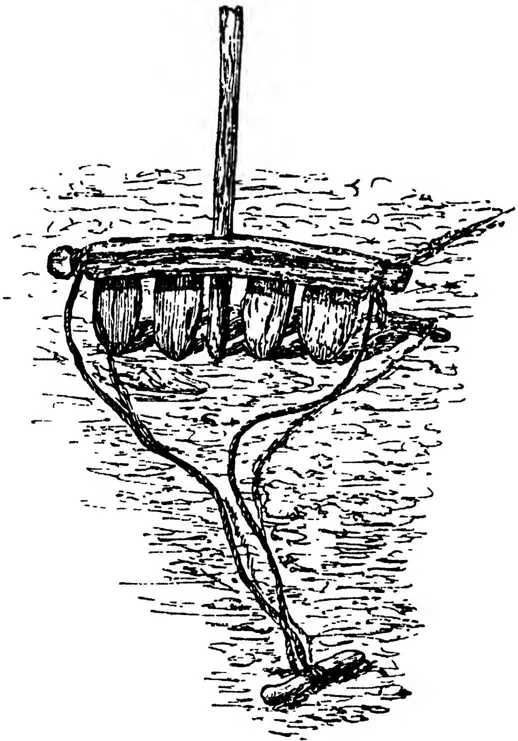


Рис. 40. Твердая пшеница «Меланопус 069», выведенная Красно кутской селекционной станцией. $^{1}/_{1}$. Рис. М. П. Лобановой.

FIGURE 37.— Hard wheat "Melanopus 069" developed by the Krasnokutsk Breeding Station. Drawn by M. P. LOBANOVA.



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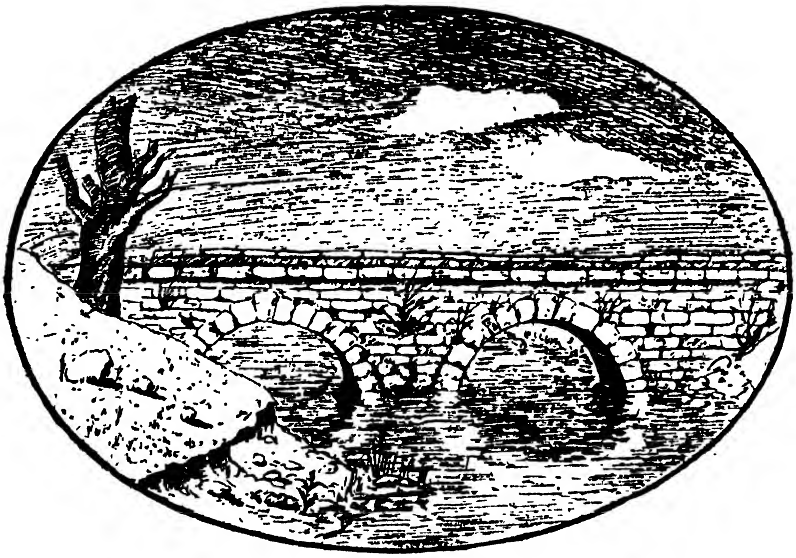

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